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DATE OF PUBLICATION: 15TH NOVEMBER, 1955

Copies may be purchased from the Secretary at 454 Christchurch Road, Bournemouth, Hants

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 12 — 15TH NOVEMBER, 1955 — PART 2

PROTECTIVE DEVICES OF ENDOPTERYGOTE PUPAE*

By H. E. HINTON, Ph.D.

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* Dr. Hinton read a shortened version of this paper, under the title "New and little-known protective devices of insect pupae," as his Presidential Address to the Ninth Congress of British Entomologists at Bristol, 23rd July, 1955.

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I. INTRODUCTION

When the evolution of any group of animals is well known, it is usually found that the aquisition of its characteristic structures and habits occured slowly and progressively up to a certain critical point, where, some aquisition being now perfected, the group was able to radiate rapidly because it could now exploit its previous environment more fully or because it could now invade environments from which it was previously barred. These critical points in evolution are often called nodal points.

In the evolution of insects there are four particularly striking nodal points. The first of these is the development of a tracheal system which enabled them to localize to some extent respiratory and humidity exchanges with the ambient air. The development of a tracheal system paved the way, so to speak, for the second nodal point, which is the aquisition of a more or less impermeable outer cuticle that enabled them for the first time successfully to invade dry terrestrial environments. The third nodal point occured when the lateral extensions of the meso- and metathorax, that had been used for gliding, were evolved into wings. This third nodal point occured in the early middle or lower Carboniferous. A short time later, geologically speaking, a pupal stage was intercalated in their life-history. This occured at the end of the Carboniferous or early Permian. The intercalation of a pupal stage in the life-history for the first time permits insects completely to dissociate the form and structure of their feeding stages from that of their reproductive and distributive stages, and, as one consequence of this new capacity, there are few environments that are not exploited by insects. At the present time nearly all of the most successful groups of insects have a pupal stage in their life-history.

In view of the enormous importance of the pupal stage for the success of insects, it is astonishing to find how little attention has been paid to it.

The complex changes that take place within the pupa and make it possible for the larva to be transformed to an adult of very different form and structure, take place more or less independently of the environment. Speaking loosely, the only demands that the pupa makes upon its external environment are that it shall have an adequate supply of oxygen and that it shall be let alone.

The insect in the pupal stage has in large measure disrupted relations with the external physical and biological environment. The variations in its structure and colour, or that of its cocoon if one is present, can in nearly every instance be easily related to its respiratory requirements, its means of defence, or the method of escape of its adult.

Its behaviour pattern is very simple indeed when compared with that of the larvae or adults. Pupae do not feed, and for this reason have neither the necessary structures nor even the simplest behaviour associated with feeding. It is true that primitive pupae have large mandibles, but, as we shall see, these mandibles are not used in feeding but only in defence or for assisting the adult to escape from the cocoon or cell. The pupal gut does not open externally and consequently there is no possibility of it taking food.

An insect in the pupal stage exhibits no social behaviour of even the most rudimentary kind nor any sexual behaviour, and, as might therefore be expected, lacks structures which in other stages are associated with social and sexual behaviour. A further important point that makes for their simplicity is that pupae either do not move at all or their capacity for locomotion is much restricted and depends entirely on structures very much simpler than the locomotory organs of other stages.

The relations established between pupae and their environment are not in every particular so simple that it is possible to discover with great ease the function of every structure of all pupae. But, from the point of view of functional morphology, the significance of the structures of the pupa are much more easily apprehended either by analogy, observation, or experiment than most of those of the larval and adult stages.

When a pupal stage is intercalated in the ontogeny of an insect, the early part of the stage that follows the pupal stage, i.e., the adult stage, always remains for a greater or lesser period enveloped by the pupal cuticle. For this reason it might be expected that some of the structures of the pupal cuticle are not related to any activity of the pupa itself but function only in that part of the adult stage which is enclosed within the pupal cuticle.

A good example of a structure of the pupal cuticle that is not functional during the pupal stage but only during the adult stage before the adult has emerged from the pupal cuticle may be seen on the pupal cuticle of caddis flies. Many of these have long fringes of hairs extending along the tibiae and tarsi. These hairs look like the so-called swimming fringes of Dytiscid larvae. Now, when the adult escapes from the pupal cell or cocoon and swims to the surface of the pond or stream, it uses only the middle pair of legs with the swimming fringes. These legs are not used in the pupal stage, nor can they be used in this stage, as the muscles that move the legs are not inserted in the pupal cuticle (Hinton, 1948). It is only when the animal lays down the next cuticle, the adult cuticle, that the muscles become inserted.

This early phase of the adult life that takes place within the pupal cuticle has been called the pharate phase of the adult (Hinton, 1946); and we may refer to an adult within the pupal cuticle as a pharate adult.

While it is important for many reasons to make a sharp distinction between the pupal stage as such and the pharate phase of the adult stage, it is also important to note that all structures of the pupal cuticle that function in respiration,* defence, or locomotion function in the same way in the pharate

* In this context is meant only the gross respiratory structures, since at one level transport through the cuticle is frequently or always affected by the activity of the attached epidermis. In the pharate adult phase the pupal cuticle is thinner than in the pupal stage and is no longer intimately connected to living cells.

phase of the adult even though the adult is now only mechanically enveloped by the pupal cuticle.

No cuticular structure appears to be known that functions in the pupal stage only and not also in the pharate adult stage, so that the rule may be formulated that *any cuticular structure that functions in the pupal stage has a similar function in the first part of the adult stage.* It sometimes happens that structures made by the larva function in defence or respiration in the pupal stage. All such larval structures function in a similar way in the early part of the adult stage.

In this paper, the various ways in which endopterygote pupae are protected from potential predators are briefly summarised. No mention is made of the numerous and interesting ways in which such pupae are protected from the exigencies of their physical environment.

II. DISTINCTION BETWEEN TYPES OF PREDATORS

In order to apprehend the full significance of certain types of protective devices a distinction must be made at the outset between two classes of predators. The most simple and general distinction between these two classes is one of size; and, broadly speaking, the large predators are chiefly vertebrates and the small ones are invertebrates. The latter are nearly always arthropods. Protection against these two classes of predators is frequently afforded by quite different structures or characteristics. For instance, some Coccinellid pupae have gin-traps, which protect them against mites and small insects, and they may at the same time have an aposematic colour pattern as a protection against the attacks of vertebrates. Failure to distinguish between the two classes of predators has in the past led to such pre-occupation with various protective devices against vertebrates that a conspicuous and generally distributed protective device like the gin-trap has only recently been noted in such common and well known pupae as those of flour beetles and lady birds.

The large predators are chiefly vertebrates that are nearly always very much larger than the pupae, and the small predators are arachnids and insects that are usually smaller than the pupae. The relations established between the pupae and these two classes of predators are reflected at various levels in the nature of the protective devices evolved against each. The simplest relation here is one of mechanical strength: a naked pupa with a smooth and heavily sclerotised cuticle may be more or less immune from the attack of any predator appreciably smaller than itself simply because such a predator is not powerful enough to break through the cuticle. It is, of course, possible that the heavily sclerotised cuticle of the large Sphingids that pupate without a cocoon in the soil, or amongst rubbish at the surface of the soil, effectively protects them against smaller lizards and birds. However this may be, it is certain from numerous published observations that the cuticle of most pupae is not strong enough to afford any protection against most of their vertebrate enemies, but it is nevertheless one of their chief defences against arachnids and insects. This point may be further illustrated: neither the amplitude of the jaws of the gin-trap, nor the force that can be provided by the muscles closing them, is sufficient for this protective device to play a part in defence against vertebrates. The rare

exception may be found when a large Sphingid pupa is attacked by a small rodent or shrew. For instance, I have found that I can sometimes get a sharp nip from the gin-trap of such a pupa by rubbing the very tip of my tongue along its sides.

Sometimes the distinction between the two classes of predators concerns merely the size of the protective device and does not also especially involve its mechanical strength. For instance, a great many moths pupate in cocoons that have an escape apparatus at the head end of the cocoon. This escape apparatus is nearly always so constructed that while it permits the moth to get out it prevents the entry of other animals. The usual solution to these contradictory demands is to construct the familiar "lobster-trap" escape apparatus. Even amongst the Saturniidae the size of the opening is such that the trap can only have been evolved against arachnids and insects.

The distinction I have made between the two classes of predators is reflected in the nature of the protective device in quite other ways than size and mechanical strength. Differences in the way the prey is recognized are correlated with the differences already noted: amongst most of the larger predators, the vertebrates, sight plays an important rôle in recognition of the prey, whereas amongst the arachnid and insect enemies of pupae sight is usually of little or no importance in recognition, which depends chiefly upon the chemical senses. For this reason procryptic, aposematic, and other colours probably rarely confer immunity against other arthropods and then probably chiefly only against some Hymenoptera.

The examples given above show some of the reasons why it is of importance to bear in mind the two categories of predators. But some protective devices afford at one and the same time protection against both classes of predators, and it is in considering the significance of these that the distinction between large and small predators is of the utmost importance. But here there is at first sight a paradox: in the type of protective device to understand the significance of which it is most important to make the distinction, the distinction may break down in that it becomes merely a distinction of size and strength without the correlated attributes already mentioned. It thus happens that we can at this level no longer consider the predators as largely vertebrates on the one hand and largely invertebrates on the other: in considering some kinds of protective devices both vertebrates and many invertebrates must be included in the category of large predators, whereas in considering other types the distinction between large and small predators must be made within the class of predators previously described as small. This is no more than to say that the significance of some sorts of protective devices is best recognized by drawing the dividing line between large and small predators at an altogether different level in the size scale. A particularly striking example of the necessity of the latter is evident when we come to consider the protective devices of the eggs of most species of the genus *Chrysopa*. The eggs of such species as *Chrysopa vulgaris* Schneider, *C. perla* L., *C. ventralis* Curtis, *C. alba* L., and *C. septempunctata* Wesm. are suspended from the lower surfaces of leaves, each on a stalk 5-8 mm. long (Withycombe, 1923). The eggs are only 0.8-0.9 mm. long, and are thus far too small to require any especial protection from vertebrates. They are also probably too small to attract the attention of invertebrates large enough to reach them

from the leaf surface. Smaller invertebrates for which they might serve as food cannot climb the slender stalks, and against those small enough to do so, such as some mites, they are probably protected by their tough chorion. Pupae protected in an analogous way are described in the section on pensile cocoons (p. 56). That both amongst invertebrates and vertebrates there is a definite size relation between predator and prey is implicit in what has been said. But here there is a difficulty: the figures generally put to this relationship are deduced or inferred from the attributes of the protective device and are not induced from observation of particular cases. This unsatisfactory state of affairs can only be remedied by experiment. If some very especial modes of feeding be excepted, such as plankton feeding, it can probably be said that no predator will normally prey upon animals below this or that per centage of its size. This sort of generalization can even now be made for a few groups of predators, *e.g.*, spiders will generally not accept prey less than one-sixth the length of their bodies (Bristowe, 1941).

III. PASSIVE AND NON-PASSIVE PROTECTIVE DEVICES

In a study of the protective devices of pupae or pharate adults it is convenient to distinguish the active from the passive. The latter involve no movements of the pupa or pharate adult but subserve their function independently of any activity of the living insect. To the category of passive defence devices belong procryptic, aposematic, and mimetic colours and shapes. This is not to say that, for instance, mimetic colours and shapes never depend for their success upon movement: in other stages the success of a particular mimitic resemblance may depend largely or entirely upon a particular pattern of behaviour. But, in so far as pupae or pharate adults are concerned, procryptic, aposematic, or mimetic colours and shapes never involve movement. We have not far to seek for a satisfactory explanation of the complete dissociation between certain types of defensive devices and movement: the history of the pupal stage is such that amongst recent endopterygote pupae the only skeletal muscles carried over from the larval stage and inserted in the pupal cuticle are the abdominal. A necessary consequence of this is that the pupa can only move its abdomen, and the type of movement possible to it is not sufficiently complex for exploitation in mimitic and other resemblances. It might be supposed that movements of the pharate adult combined with particular colours or shapes of the pupal cuticle would sometimes be involved in a mimitic resemblance, but all exposed pupae—the only pupae that could be concerned in such a resemblance—are obtect; and the adult within can therefore effectively produce no more complex movements of the pupal cuticle than can the pupa itself.

The term allaesthetic was proposed by Huxley (1938) for characteristics, ". . . which exert their biological effect via the distance receptors of another individual, i.e., those of smell, hearing and sight." To group protective devices into allaesthetic and non-allaesthetic immediately involves the difficulty that the sound producing organs would have to be classed in both of these categories: in fact, it is quite possible that the stridulatory organs of pupae exert their chief effect by producing waves of pressure transmitted either through the substrate or by direct contact and do not exert their most important effect through the distance receptors of other animals.

IV. PASSIVE PROTECTIVE DEVICES

A. General protective devices of cocoons*

Where an escape apparatus is built into the cocoon, it is nearly always so constructed that it prevents the entry of small enemies, as is well exemplified by the widely distributed "lobster-trap" apparatus. A very large number of cocoons have no escape apparatus; and amongst those species that have adecticous pupae and non-functional adult mandibles, or at least adult mandibles not capable of making a hole in the cocoon, a number of very especial methods of escape have been evolved (summary in Hinton, 1946a). It seems not unreasonable to suppose that an escape apparatus, however it may be constructed, is not quite as effective a barrier against enemies as an intact cocoon; and it may be that the especial methods of emergence of species without functional adult mandibles and with adecticous pupae are brought about by the need for greater protection than can be provided by any escape apparatus. For instance, in the Saturniidae it would seem that the primitive cocoon is that with the "lobster-trap" or "eel-trap" escape apparatus, and that the intact cocoon together with the especial method of escape (cocoon-cutter on adult wing; cocoon-softening fluids secreted by adult) are secondary features evolved in response to a greater need for cocoon protection.

It is not uncommon to find that when a cocoon is fastened to a leaf that is likely to drop or be blown off before the emergence of the adult, the leaf is bound by silk to the twig or both leaf and twig are bound to the branch. The larvae of the Oriental Lycaenids, *Virachola isocrates* F. and *V. perse* Hew., feed in a number of different kinds of fruits. Both species normally pupate within the fruit. As the larva develops and destroys the fruit, the latter is prevented from falling to the ground or being blown off the tree or bush in a most interesting way. At intervals the larva crawls out of the fruit and climbs down the stalk to the branch, and there it binds the stalk to the branch with silk. It then climbs up the stalk and enters the fruit to feed for

* There is some evidence to suppose that the larva of the common ancestor of the Endopterygota utilized a product of its labial glands in the construction of a resting place for its pupa: either it made a cocoon, or lined its pupal cell with silk, or used its labial glands in cementing or binding together the walls of its pupal cell. Amongst the Hymenoptera and Panorpoidea the numerous exceptions to this habit are clearly secondary. However, the whole of the super-order Neuropteroidea (Megaloptera, Neuroptera, Coleoptera (Strepsiptera ?)) lack labial glands in the larval stage. Labial glands are a primitive feature of pterygote larvae. It may be supposed that the loss of labial glands in the larval stage of the common ancestor (they are present in the adult stage) occured because they ceased to be of selective value. Now, the chief value of the labial glands in the larval stages of endopterygotes (if recent forms are any guide) was in the construction of shelters for the larvae and cocoons for the pupae. Both could be dispensed with by a larva living in the earth or in wood; and it is only such environments (or endoparasitic, which are excluded on other grounds) which are likely to account for the change from developing the wings outside the body to developing them inside the body. The presence of labial glands in the larvae of other endopterygotes may be an indication that their ancestors quit a life in the earth or wood sooner than the ancestors of the Neuropteroidea. Amongst recent Neuropteroidea there are many that construct a silken pupal cocoon, but the habit is in every instance a secondary one in the superorder. The silk used for the pupal cocoon is produced by the Malpighian tubes in the Neuroptera and some Coleoptera, whereas in other Coleoptera the silk is produced by glands in the posterior abdomen.

another period. This is repeated again and again until the fruit is so securely fastened to the branch that it may require some effort on the part of a man to detach it. When a fruit is large enough to accomodate several larvae, *e.g.* pomegranate, all of them assist in securing the fruit to the branch (Bell, 1920).

Sometimes when the cocoon is attached to a small twig, a loose tangle of silk and poison-containing setae is constructed around the twig above and below the cocoon, as in some tropical Lasiocampidae. Caterpillars with poison setae frequently incorporate these into the fabric of the cocoon. The poison contained in the lumen of the specialised setae does not appreciably lose its activity. The use of poisonous hairs in cocoon protection is known in the Megalopygidae, Eucleidae, Lymantriidae, Thaumetopoeidae, and other moths.

Calcium compounds extracted and stored by the Malpighian tubes are sometimes used to harden the cocoon, *e.g.* the cocoon of *Antheraea pernyi* Guèr. is hardened by calcium oxalate, whereas that of species of *Malacosoma* is hardened with calcium carbonate. In some beetles the pupal cell is lined with a fairly thick layer or cocoon of calcium carbonate, *e.g.* Cerambycini (*Plocaederus*, *Diorthus*, *Dialeges*) and Oemini (*Xystrocera*) in the Cerambycidae.

1. Pensile cocoons

The cocoons of some insects are suspended by a silken cord from a twig or leaf. The principles that underlie this method of defence have already been discussed in relation to the stalked eggs of *Chrysopa* (p. 53). Perhaps the best known of these pensile cocoons are those of the large silk moths of the family Saturniidae. Among the species that have pensile cocoons are *Coscinocera hercules* Miskin, *Callosamia promethea* Drury, *Philosamia cythia* Drury, *Antheraea mylitta* Drury, *A. yamamai* Guèr., and the species of *Rhodinia*, *Rothschildia*, and *Attacus*. All species of some genera have pensile cocoons, whereas in other genera, *e.g. Callosamia* and *Antheraea*, some do and some do not. The pensile cocoons may be naked or more or less enclosed by leaves fastened to their surface, as in some species of *Rothschildia* and *Attacus*.

The pensile cocoons of the Saturniidae, especially those that are naked or partly so, are easily distinguished under natural conditions by humans and perhaps also by birds. Nevertheless, there seem to be no records of any being effectively attacked by birds: birds large enough to open the tough cocoons are either unable to obtain a purchase near enough, or, if they can do so, the cocoon simply swings away when pecked and so escapes damage. For instance, Webster (1904) was unable to find any cocoons of *Philosamia cynthia* which had been damaged by woodpeckers or other birds, but he did find that in the same region non-pensile cocoons of other species of Saturniidae were often destroyed by woodpeckers. In this connection it is interesting to note that on one occasion Carpenter (*in* Ford, 1955) found a colony of *Zygaena filipendulae* L. in which some of the cocoons had been attached to a wire fence and others to tall grasses; and all those on the fence had been pecked open by birds, whereas those on the grass stems, on which the birds could obtain no foothold, escaped damage. That the pensile cocoons of the Saturniidae simply swing away when pecked at by birds and so

escape damage has also been noted by other writers (*e.g.* Sevastopulo, 1949).

In a few species both pensile and non-pensile cocoons may be produced, and the difference may be individual, racial, or it may depend upon some environmental factor. The Saturniid, *Telea polyphemus* Cramer, may spin a band of silk along the petiole of one of the leaves in which it is enclosed up to the stem and then ring the stem with silk. Such stalked or pensile cocoons do not fall to the ground when the leaves wither and are detached. The same species may, on the other hand, spin amongst the leaves and construct no silken band or stalk so that when the leaves are detached the cocoon falls to the ground. In New York the cocoon of *Telea* is usually pensile, but in Indiana it is nearly always so (Soule, 1905). Out of 335 cocoons from Chicago only 40 were pensile (Kuschel, 1906). Cockle (1904) claims that in regions of heavy snows, *e.g.*, Montreal, the cocoons are usually non-pensile, whereas in warmer climates such as in western North America, they are usually pensile. Kunzé (1906), on the other hand, claims that in New York the cocoons are pensile on maple but are nearly always non-pensile when spun on white birch. He found that on "swamp oak" they were always pensile, whereas about a mile away on white birch on higher ground they were non-pensile. According to him, those on the higher ground would all drop during winter gales, whereas had they been similarly constructed on swamp oak they would have fallen into the water.

Perhaps the most remarkable of all pensile cocoons are those of the Central and South American Yponomeutidae of the genus *Urodus* H.-S. (=*Trichostibias* Zell.). *U. isthmiella* Busck is one of the largest species of the genus. Its obovate cocoons are 1.9 cm. long and are suspended from a leaf by a silken cord over 32 cm. long. The silk of both the cord and cocoon is a bright salmon red. The walls of the cocoon are an open meshwork with thick parallel threads about 1.5 mm. apart and finer cross threads about 1 mm. apart. The posterior end of the cocoon terminates in a short open neck through which the larval cuticle is pushed out by the pupa, thus, as Busck (1910, p. 528) says, ". . . insuring a clean, airy habitation, free from anything that might become water-soaked, or by its smell attract ants, that ever present enemy of insect life in the tropics. The entire elaborate contrivance is presumably a very effective protection against ants during the defenseless pupa period, for even should an ant attempt to climb down the long suspending thread it would probably be shaken off by the lusty violent jerks of the pupa, which were observed in the present specimen, whenever it was disturbed." Cocoons of other species of *Urodus* have been described by Strand (1911), Walsingham (1897), and others. From the figure given by Bates in "*The naturalist on the river Amazon*" of a pensile, rose-coloured cocoon found by him at Ega, it seems certain that he had before him a species of *Urodus* and not a Lithosiid, as he believed.

A few Braconids have stalked or pensile cocoons. The best known of these are species of *Meteorus*, some of which may be suspended from a leaf or twig by a silken cord up to eight inches long, *e.g.*, *Meteorus pulchricornis* Wesmael (Clausen, 1940). Unlike the pupae mentioned above, those of *Meteorus* always have their head downwards at the end of the cocoon opposite the point of attachment of the cord. One species of *Apanteles*, *A. formosus* Wesm., is known to construct a stalked cocoon.

No attempt is made here to enumerate the protective devices of social insects which also effect the protection of their pupae, but it may be mentioned in passing that some of the social insects have pensile nests. Some of the best known of these are wasps of the genera *Stenogaster* and *Polybia*. Some of these are regularly associated with stinging ants. For instance, in South America species of *Polybia* regularly build their nests in trees where ants of the genus *Azteca* also nest, and some birds also regularly build their conspicuous pensile nests in trees protected by both ants and wasps (summary in Myers, 1935).

2. Adaptive colours of cocoons

Aposematic and pseudaposematic cocoons are rare—I know of no certain examples—and few cocoons have a special protective resemblance to another object. Instances of the latter phenomenon are listed on p. 65. Most exposed cocoons are procryptic either because of their colour or shape, or both, or because the larva fastens on the outer surface bits of material taken from the immediate environment: different species fasten leaves, pieces of bark, fragments of fungi or lichens, bits of earth, and so on according to their circumstance; and such cocoons can so resemble their background as to be more or less indistinguishable from it by predators that depend upon sight. Attention has been drawn by other writers to the fact that cocoons which contain pupae in the winter are generally better concealed than summer cocoons. Poulton (1890) suggests that this is due to the fact that insectivorous animals are often pinched by hunger in the winter and might therefore attack cocoons they would leave alone when insects were more readily available.

The procryptic colour of some, possibly many, cocoons is adjustable according to the background—the colour of the reflected light—to which the larva is exposed during or shortly before spinning. For instance, *Saturnia pavonia* L. is said to spin dark brown cocoons when in a black bag and white cocoons in white surroundings in a strong light (Poulton, 1887a). There is some slight evidence that some species will alter the colour of the cocoon during spinning if they are exposed to a dark and then to a light background, *e.g.*, the Phalaenid, *Halias prasinana* L. (Poulton, 1887b). The Geometriid, *Opisthograptis luteolata* L. (Poulton, 1888), and the Lasiocampid, *Eriogaster lanestris* L. (Poulton, 1890), also appear to be able to adjust the colour of their cocoons according to outward circumstance. Clearly more experimental work on this subject is urgently required.

Sometimes the colour of the cocoons would appear to be of no selective value. For instance, amongst the races of the silkworm, *Bombyx mori* L., are many that may be distinguished by the colour of their cocoons: white, yellow, golden, greenish, rose, and so on; and there are no wild populations of this insect. It is now known, chiefly as the result of the work of Jucci and Manunta, that these differences of cocoon colour are due to racial differences in the kind, quantity, and speed of absorption of pigments by the silk glands. These are chiefly carotenoids but also include some flavones such as anthoxanthins. These pigments are derived from the food and must be liberated by the gut epithelium into the blood. Thus, racial differences in cocoon colour exist where the absorption attributes of the silk glands are similar but differences exist in the gut epithelium.

B. Retention of larval cuticle by pupa

The pupae of a large number of groups retain the larval cuticle. They may be entirely enclosed within it, or the cuticle may be only attached to the last few abdominal segments of the pupa. The biological significance of this habit varies so greatly that no general statement can be made as to its selective value. Where the habit has been investigated, the particular nature of its significance has usually been easily apprehended by observation or experiment, and for this reason caution must be observed in too readily supposing that the habit is without significance—is accidental—in those instances where its significance is still not known.

In this section I am only concerned to draw attention to the diverse ways in which the larval cuticle affords the pupa or pharate adult protection. Sometimes the protection afforded by the retention of the larval cuticle depends upon some activity of the pupa or pharate adult; and instances of this are discussed in others sections on pp. 85, 89.

The Diptera-Cyclorrhapha are by far the most numerous group that retains the larval cuticle. In these the cuticle of the third or penultimate instar is hardened and forms a kind of cocoon, called a puparium, which is probably impervious to the attacks of most small predaceous insects and mites. The Cyclorrhapha are probably the most successful group of insects, and it is hard to suppose that their great success is not in some measure due to their exceptional method of protecting their pupae. In at least two groups of aquatic species the shape of the puparium may itself be of some value against predators. In Muscids of the genus *Limnophora* the spiracles of the eighth abdominal segment are borne on long processes, and the prolegs of the same segment are very long and are directed forwards. When the cuticle of the third instar is hardened, the orientation forwards of both the spiracular processes and the prolegs is maintained with the result that these four appendages form an anchor. The larvae pupate amongst moss, often in the swiftest part of streams. The posterior anchor not only prevents them from being washed downstream, but also makes them difficult to detach from the moss and may in this way sometimes save them from predators. In some Ephydridae, such as *Ephydra subopaca* Loew and other species of the genus, the cuticle of the third instar is normally hardened while the larva grips a stem or other object on the surface between the prolegs of the sixth and eighth abdominal segments. Thus, when the puparium is finally formed, it is very firmly attached. The chief selective value of this habit may be to prevent the puparia from drifting onto the shore, but their firm attachment probably affords some protection against fish and other predators.

The pupae of some other insects also remain entirely enclosed within the larval cuticle, but in these others it is that of the last and not the penultimate instar. The most numerous group with this habit are the Stratiomyidae, which are unusual in that the larval cuticle is impregnated with calcium carbonate, sometimes up to as much as 75% by weight (Müller, 1925). Apart from the Stratiomyidae, only the occasional species in other groups remains entirely within the larval cuticle, *e.g.*, the Indo-Australian Lycaenid, *Liphyra brassolis* Westw. The examples given below illustrate the extreme diversity in the way in which protection is afforded by retention of the larval cuticle.

1. Protection by warning colour of larval cuticle

The caterpillar of the African Lasiocampid, *Chrysopsyche varia* Walk., is aposematically coloured. It spins a cocoon with a small hole in the posterior end. When the pupa sheds the larval cuticle, it pushes it out through the posterior hole, but the cuticle remains attached and presumably its brilliant warning colour affords the pupa some protection (Poulton, 1912d).

2. Protection by defensive fluid in larval cuticle

The larvae of the genus *Forcipomyia* are apneustic, secondarily terrestrial Ceratopogonidae. On the head, thorax, and abdomen there are paired, usually spatulate, setae through which a substance is secreted which extracts water from the atmosphere. The larvae are normally found in very humid environments. In such environments, water absorbed by the substance at the tips of the specialised setae causes a drop of solution to appear at the tip of each seta. When the larvae are placed in saturated environments (over 95% R.H.) drops of the solution run down the setae and wet the cuticle. Keilin (1918), who appears to have been the first to comment on the biological significance of the specialised setae, supposed that the hygroscopic substance collected water from the atmosphere which then wetted the cuticle and in some way facilitated respiration. Since the larvae are apneustic, the cuticle must be relatively permeable to air, and an hygroscopic film over the surface might be expected to tide the larvae over when exposed for short periods to lethal humidities. Keilin's explanation of the function of the setae was repeated by Saunders (1924), and Keilin (1944) quotes Saunders as an authority for the view first published by himself. The functional significance of the substance secreted through the specialised setae was investigated by myself and some of my students. Here it is only necessary to state that we have found that the substance is defensive in function and appears to have no significance in respiration. Experiments (by M. F. Jenkins) with a colony of *Lasius niger* L. established in the laboratory, showed that the ants would attempt to attack larvae of *Forcipomyia nigra* Winnertz. Whenever they came close enough to bite, they touched one or more droplets, upon which they immediately dropped the larvae and usually spent several minutes cleaning themselves. At one time the colony was fed only from a wooden platform in one corner of the tank in which it was housed. At intervals of 24 hours or more a *Forcipomyia* larva was substituted for sugar or for a dipterous larva of similar size that had proved acceptable to the ants (*e.g. Ditomyia* sp.) In each instance the *Forcipomyia* larva was quickly dropped, and the ant that had picked it up spent some minutes cleaning itself. Preliminary experiments at different humidities indicated that at low humidities, when droplets were not formed, the larvae were dropped less quickly by the ants than at high humidities when large droplets were on the apices of the setae.

The pupae do not completely shed the larval cuticle, which is retained over the posterior abdominal segments. Enough of the hygroscopic substance is contained in the setae (or in the reservoirs at their bases?) so that in saturated or nearly saturated environments large droplets are formed on the apices of the specialised setae. Experiments with ants showed that if the larval cuticle was removed, the ants would carry the pupae into their nest.

When the ant approached a pupa from in front, it sometimes succeeded in dislodging it from the larval cuticle and would then carry it away. Quite often, however, the ant would come into contact with one of the droplets, and it then behaved as if it had attacked a larva. When the ants approached the pupae from the side or from behind, they always became smeared with the hygroscopic substance and retired and cleaned themselves. The nature of the hygroscopic substance is not known. The pH of one of the droplets is 6.0-7.0, according to dilution. It is not known if it is poisonous to ants or if, as seems probable, its chief effect is due to its sticky nature.

The larvae of *Forcipomyia* usually pupate in groups so that the pupae are found in small circles with their heads pointed towards the centre. A possible explanation of this habit, which has been commented upon by many, now becomes obvious for the first time: when pupae are in such circles, the potential attacker is presented with a more or less complete ring of larval cuticles containing the defensive fluid.

3. Protection by setae or spines of larval cuticle

The pupae of a number of species of Dermestid beetles never shed the larval cuticle although the cuticle splits open dorsally, *e.g.*, the Trinodinae (*Trinodes*) and some Anthreninae (*Anthrenus*, *Thaumaglossa*). The larvae of these as well as those of most Dermestids are densely clothed with long spinulose setae. The pupa splits the larval cuticle along the cleavage line as usual, but the split generally extends further posteriorly. For instance, in *Anthrenus* the split is continued to the hind margin of the sixth abdominal segment and sometimes even to the hind margin of the eighth. In *Anthrenus* the dorsum of the head, thorax, and abdomen is exposed (fig. 1). The exposed areas of the pupal cuticle are densely clothed with long, fine hairs which are sometimes so entangled that they form a thick mat, whereas those parts that are concealed by the larval cuticle have only very short, erect, and inconspicuous hairs. Sometimes, as in *Thaumaglossa bimaculata* Arrow, the last larval instar has very long and fine hairs on either side of the cleavage line. These hairs meet and are entangled above the exposed parts of the pupa so that a fairly thick mat is formed. The exposed parts of the pupa are thus in some species protected by both larval and pupal hairs, and the larval hairs also make it difficult to dislodge the pupa from the larval cuticle.

Of the three genera mentioned, only living pupae and pharate adults of *Anthrenus* species have been available. These do not wriggle the abdomen even when pricked hard enough to be seriously damaged. It has been shown (Hinton, 1946b) that in this family the primitive pupa has five or six dorsal, unpaired gin-traps. Both pupae and pharate adults of the primitive forms can, of course, wriggle the abdomen. The gin-traps (and perhaps also the mobility of the abdomen) are independently lost in the Trinodinae and Anthreninae, and both have evolved a similar and highly specialised method of protecting the pupa and pharate adult.

The spines or setae of the larval cuticle probably also sometimes afford protection even when the larval cuticle is only attached to the most posterior segments of the pupa, as, for instance, in the Lycaenid, *Epitola hewitsoni* (Eltringham, 1923).

C. Protective colours of pupae

1. Concealing colours and shapes

Perhaps the chief means of defence of most large exposed pupae against vertebrates are procryptic or disruptive colours or tones, which are frequently combined with alterations of shape that subserve the same function. This phenomenon is so familiar that there is here no need to cite examples.

In many species of butterflies individual pupae may be differently coloured. The factors that in some species determine this individual variability are not known, but in a number of species it has been shown that the colour of

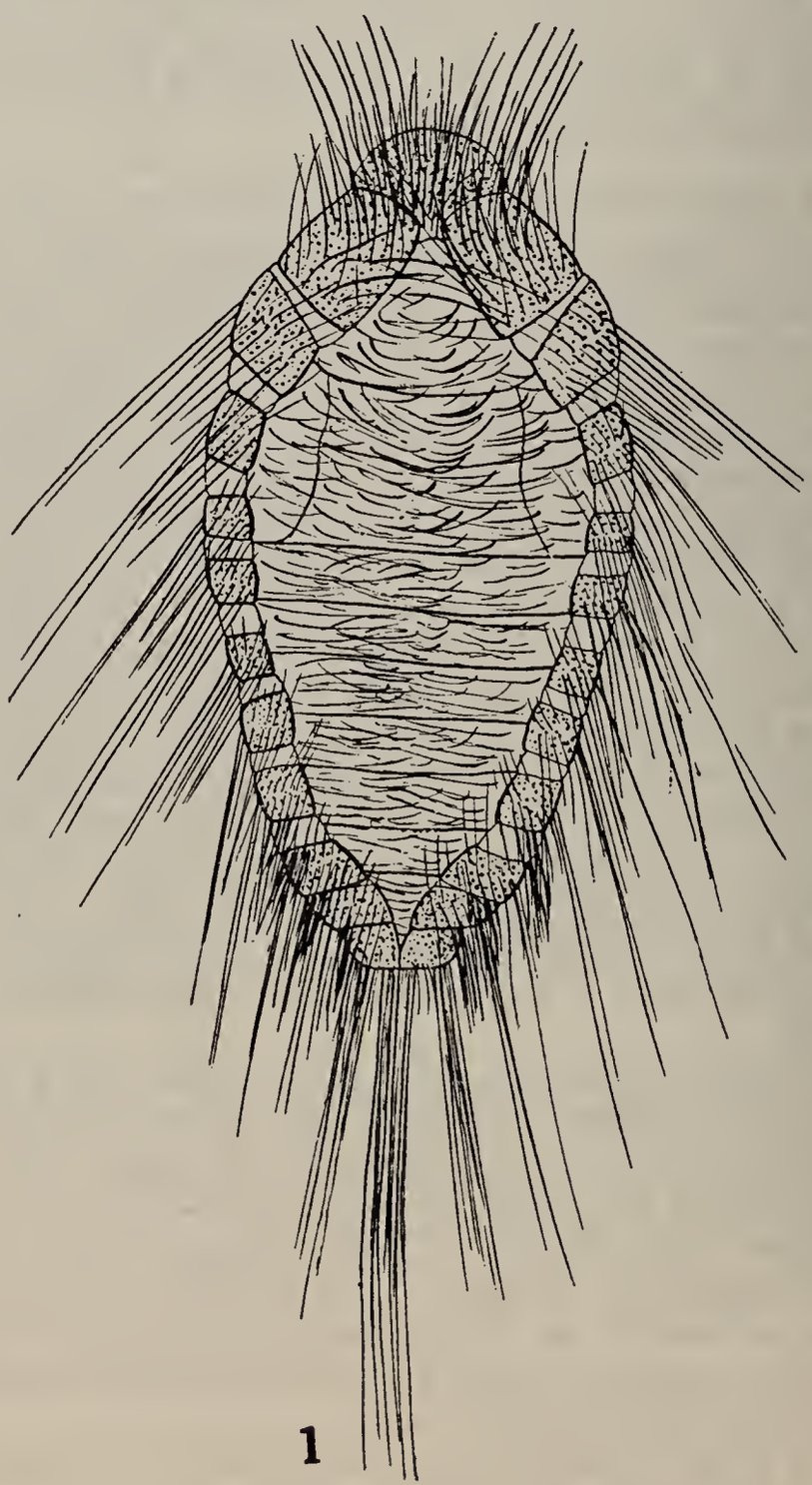


Fig. 1. Dorsal view of the pupa of *Anthrenus vorax* Waterhouse enclosed in the last larval cuticle. (After Hinton).

the pupa depends upon the colour of the background, that is the colour of the reflected light, to which the larva is exposed shortly before pupation. This was first shown for *Pieris brassicae* L. and *P. rapae* L. by Wood (1867). The capacity of these species for adjusting their protective resemblance was confirmed by Poulton (1887, 1887a, 1890) and many later writers, and is now known to occur not only in many species of butterflies, especially Papilionidae, Pieridae, and Nymphalidae, but also in some moths which pupate in cocoons of so open a meshwork that the pupa within can easily be seen, *e.g.* the Geometriid, *Ourapteryx sambucaria* L. Determination occurs in the larval stage and not in the pharate pupal stage: this is why Poulton's stage "iii" larvae of *Aglais urticae* L. were not as sensitive as stage "ii" larvae, since the former stage includes both the end of the larvae stage and the pharate pupal stage.

In *Pieris brassicae* L., for instance, exposure to green, yellow, or orange light causes the suppression of black and white pigments so that the pupae are plain green; and this influence is transmitted so that the following generation tends to produce green pupae even when not exposed to green-producing light (Dürken, 1923). Covering the eyes with black pigment does not affect the capacity of adjustment in *Aglais*, but the response is eliminated if the larva is decapitated or the eyes cauterized, which seems to show that either the eyes or some other centre in the head controls the response. A brief summary of some of the relevant literature on this subject is given by Wigglesworth (1953).

2. Warning colours

A number of aposematically coloured pupae are known, *e.g.* those of many Coccinellidae, Chrysomelidae, and that of the magpie moth, *Abraxas grossulariata* L. The pupa of the magpie moth is especially interesting in that although it is aposematically coloured it is enclosed in a cocoon, but the meshwork of the cocoon is sufficiently open so that the pupa within can be seen without difficulty. Experiments with this pupa show that it is very generally rejected by birds, as are its larvae and adults which are also warningly coloured. However, larvae and pupae are accepted by the cuckoo (White, 1935). In *Chrysomela tremula* F. (Hinton, 1951) the aposematic pattern of the retained larval cuticle is continued on the pupal cuticle in such a way that it enhances the continuity of pupa and larval cuticle (fig. 23). Many tropical butterflies have pupae with bright metallic colours, which are often very conspicuous, even at a distance. These are sometimes said to be warningly coloured, but most are probably cryptically coloured, as Poulton suggests. Many of the aposematic pupae belong to synaposematic assemblies, *i.e.*, groups of unrelated insects that are found in the same environment, have similar warning colours, and are also distasteful.

I am aware of no pseudaposematic pupae unless certain instance of special protective resemblance, *e.g.* pupae that resemble the heads of snakes, be included in this category. Before it is possible correctly to describe a pupa as pseudaposematic it has to be demonstrated that (a) it is edible to some of the predators to which it is normally exposed in nature, and that (b) its colours evoke an avoiding response in these.

D. Special protective resemblances

The theory of protective colouration is still hotly disputed by many who are in no way inhibited by lack of experience of animals in nature nor by a slight knowledge of past and present literature on the subject. Accounts of special protective resemblance now as in the past prove particularly attractive to the critic. We must recognize that implicit in most of the accounts of special protective resemblance is the assumption that because, say, a caterpillar is indistinguishable from sticks to the human observer it is therefore also indistinguishable from sticks to birds and other animals that depend upon sight. In other words, the naturalist has generally assumed that what at close range and in a good light deceives him will also deceive some or most of the vertebrates that rely upon sight for detecting their prey. To some this appears to be a reasonable assumption, especially when it is not forgotten that the naturalist's knowledge of form and structure is altogether beyond that of any bird or other animal. Unfortunately for the critics, the assumption has been found to be correct whenever tested, *e.g.* the recent work of Ruiter (1952) on the resemblance of Geometriid larvae to sticks.

As a good illustration of the kind of attack usually made upon the theory of protective colouration, Thompson (1942, p. 958 *et seq.*) may be quoted: in content it is similar to most other attacks on the theory, but, unlike many, it is elegantly worded. "Only for a moment let us glance at a few instances by which the modern teleologist accounts for this or that manifestation of colour, and is led on and on to beliefs and doctrines to which it becomes more and more difficult to subscribe."

"Some dangerous and malignant animals are said (in sober earnest) to wear a perpetual war-paint, in order to 'remind their enemies that they had better leave them alone.' The wasp and the hornet, in gallant black and gold, are terrible as an army with banners; and the Gila Monster (the poison lizard of the Arizona desert) is splashed with scarlet—its dread and black complexion stained with heraldry more dismal. But the wasp-like livery of the noisy, idle hover-flies and drone-flies is but stage armour, and in their tinsel suits the little counterfeit cowardly knaves mimic the fighting crew."

"The ptarmigan and the snowy owl, the arctic fox and the polar bear, are white among the snows; but go he north or go he south, the raven (like the jackdaw) is boldly and impudently black."

". . . And a flock of flamingos, wearing on rosy breast and crimson wings a garment of invisibility, fades away into the sky at dawn or sunset like a cloud incarnadine."

"To buttress the theory of natural selection the same instances of 'adaptation' (any many more) are used, as in an earlier but not distant age testified to the wisdom of the Creator and revealed to simple piety the immediate finger of God."

This kind of argument sounds formidable and is sometimes convincing to zoologists who have made no close study of animals in their natural environment and who are, perhaps, less interested in animals than in exploiting the capacities of new gadgets. The emotional language in which his attack is couched is only equalled in the wildest passages of the most uncritical adherents of the theory of protective colouration.

A widely practised technique of vilification is that which seeks to include

what is to be vilified in a category of events already discredited in order to avoid the difficulty of dealing faithfully with the argument. Teleological argument is discredited: if the theory of protective colouration be described as teleological the unwary may think there is no need to look further into the matter and so the gratuitous nature of the classification may escape their notice.

A further example of illegitimate argument is to lump dissimilar cases together under the pretension that the same evidence applies to each. That Thompson does just this is evident when he asks why if other animals are white in the arctic the raven should be black and successful. But each animal has its own especial relations with the outside world. The raven is an omnivorous scavenger with few or no enemies in the arctic and thus no selective pressure is exercised against its black colour as is against any other colour but white in the ptarmigan and, for different reasons, in the arctic fox, polar bear, and snowy owl. His argument could be used to maintain that the poison glands of snakes are of no value to them because non-poisonous snakes are also successful.

Great theories like great causes seem to attract to themselves extravagant enthusiasts. They have their honest and dishonest critics, their competent as well as incompetent critics. An unscrupulous attack upon a theory may usually be recognized for what it is by a feature that is common to nearly all such attacks: the central theme of the theory and the chief evidence is ignored but instead the extravagances of already discredited adherents are demolished with gusto. This kind of intellectual sleight of hand, and it is no more than this, is glaringly evident in his passage relating to the colour of flamingos, which is from the justly discredited work of Thayer.

Thompson feels called upon to cite some field naturalists in support of his argument. Theodore Roosevelt and two others, not very well known as naturalists, are cited—not Darwin, Müller, Wallace, Bates, Belt, Poulton, nor any other great nineteenth or twentieth century naturalist but Theodore Roosevelt!

1. Special protective resemblances of cocoons

(a) *Resemblance to an empty cocoon.*

Euproctis lanaria Holl. (Lymantriidae) of West Africa spins its golden-yellow and very thin-walled cocoon on the surface of a green and living leaf. The cocoon has two compartments, a high upper one and a small lower one separated by a thin sheet of silk. The pupa, which is green like the leaf, is contained in the lower compartment. It is quite easy to see into the cocoon, which appears to be empty because the procryptic colour of the pupa prevents its easy recognition (Lamborn, 1913).

(b) *Resemblance to cocoon from which parasitic wasps have emerged.*

Caterpillars of several unrelated families attach to the surface of their pupal cocoons structures that resemble the cocoons of parasitic wasps. These structures, usually called false cocoons, generally resemble Braconid cocoons. After consuming their host, the brood of Braconid larvae frequently emerge and spin their own cocoons to the surface of their host's cocoon. It is often stated that birds do not in fact open cocoons that have Braconid cocoons attached to their surface. Such statements about the

habits of birds are based on rather casual observations and therefore, although they are probably quite correct, require confirmation. It is supposed that each bird soon learns that there is little or nothing but the skin of an insect left in cocoons so adorned, and the individual parasites are not sufficiently large to repay the effort of opening their cocoons. The resemblance to cocoons parasitised by wasps may be very close, and on at least one occasion an entomologist was deceived into throwing away the cocoons of an Arctiid, *Deilemera antinorii* Oberth, believing them to be parasitised (Poulton, 1912b).

The construction of cocoons that resemble parasitised cocoons is recorded in the following families:- Gracilariidae: *Epicephala chalybacma* Meyr. of Ceylon and India (Green, 1913; Fletcher, 1920); *Marmara salicitella* Clem. (Clemens, 1863), *M. opuntiella* Busck (Busck, 1907), and other species of the genus (Forbes, 1923; Poulton, 1912c), and *Acrocercops strigifinitella* Clem. and other species of the genus from North America and the Oriental Region (Forbes, 1923; Fletcher, 1920); oriental Zygaenidae: *Lophosoma quadricolor* Walk. and undetermined species of *Artona* and *Phacusa* (T. R. Bell, unpublished notes); African Arctiidae (Hypsinae): *Deilemera antinorii* Oberth. (Lamborn, 1912, 1913; Poulton, 1912, 1912b) and *D. leuconoe* Hopff. (Poulton, 1912b); and the West African Bombycid *Norasuma kolga* Druce (Poulton, 1912a, 1930). A brief summary of some of these examples is contained in Poulton (1931).

The way in which the false cocoons are made may be much the same in different families. The most detailed description of their construction is that of Green (1913) for *Epicephala chalybacma* Meyr. The larva voids *per anum* a globular pellet apparently composed of a number of "dried bubbles." The pellet is then attached by a silken cord to the inner roof of the cocoon. After this, the larva bites a hole in the cocoon near the point of attachment of the cord and pushes the pellet out through the hole. When the pellet is on the outer surface of the cocoon, the larva repairs the hole through which it was pushed. During this process the larva has reversed its position in the cocoon, and, after a short pause, a second pellet is voided and fastened in the same way to the opposite end of the cocoon. The number of pellets or false cocoons thus formed varies, but on one cocoon more than forty were counted. *Norasuma* produces similar pellets of dried bubbles, but these are produced on the surface of a loose silken network. After they have been attached by silken cords, the larva crawls beneath the network and there spins its cocoon. *Deilemera* also produces its false cocoons on the surface of a loose network beneath which it pupates. Each of its false cocoons usually consists of two or three pellets of dried bubbles tied together. The nature of the so-called dried bubbles and the way they are formed is not known.

(c) *Resemblance to a drop of water.*

The larvae of many but not all Limoniini (Tipulidae) secrete large amounts of a hygroscopic protein from their labial glands, which are usually very large as compared with those of other Tipulidae. The larval as well as the pupal and pharate adult stages may be surrounded by a considerable quantity of this protein, the chief function of which would seem to be to dampen down temporary fluctuations in the humidity of the ambient air. The

hygroscopic protein layer probably permits the insect to survive for short periods at humidities that would otherwise kill it. It probably also functions as a protective device. The pupal and pharate adult stages may be passed in a more or less discrete cocoon or case within which the insect is imbedded in the protein, or a discrete outside case may be absent. When the latter is the case, the insect is simply imbedded in the jelly-like protein. Hingston (1932, p. 342) claims that an undetermined species of *Geranomyia* in the rain forests of British Guiana pupates in a ball of jelly which is attached to the end of a Turu palm leaf and looks like a drop of water about to fall off the end of the leaf.

2. Special protective resemblances of pupae

(a) *Resemblance to snakes.*

A large number of caterpillars, especially those of the family Sphingidae, are well known for their resemblance to snakes, but I am aware of only one pupa that looks like the head of a snake. According to Bingham (1907), the pupa of the Oecophorid, *Tonica barrowi* Bingh. (=*Binsitta barrowi*) of Burma bears a very close resemblance to the head of the wolfsnake (*Lycodon aulicus* L.), a bird-eating snake common in Burma and widely distributed in the Oriental region.

(b) *Resemblance to monkeys.*

Some Lycaenid pupae have attracted much attention owing to their resemblance to a monkey's face. The Oriental *Spalgis epius* Westw. (fig. 2) resembles the common rhesus macaque (*Macaca mulatta* Zimm.) of its region. The African *Spalgis lemolea* Druce (fig. 3) bears some resemblance to a chimpanzee, and some resemblance may be seen between the pupa of *Fenisca tarquinius* F. of North America and some of the Cebidae.

(c) *Resemblance to a pupa from which parasites have emerged.*

The pupa of an African Lycaenid, *Agriolaus maesa*, has on its surface depressed areas which are coloured black and are said to resemble the holes made by parasites that have emerged. It has been claimed that this pupa mimics a gall from which the gall insects have already emerged (Eltringham, 1923). Experiments have shown that birds will open certain types of galls from which the parasites have not emerged but will not open the same galls from which parasites have emerged. It is not known how birds distinguish between inhabited and uninhabited galls, but it is supposed that they are either guided by the exit holes of the parasites or by a difference in sound when the galls are tapped. However this may be, pupae that have been consumed by parasites are common enough in nature, and it is not difficult to suppose that birds learn to recognize these by the obvious exit holes of the parasites. Eltringham's supposition that the pupa of *A. maesa* resembles a gall rather than a pupa from which parasites have emerged seems to be unnecessary.

(d) *Resemblance to a pupa attacked by moulds.*

The pupa of a West African Lycaenid, *Teratoneura isabellae* is so clothed with whitish setae that it appears to be heavily attacked by moulds. It is described by Eltringham (1923, p. 89) as follows: "Though fairly recognizable as a chrysalis, it is covered with minute growths of a whitish colour,

and in addition there are (growing apparently from various points) longer projections of a more or less fungoid appearance. The general effect is to give the impression that the creature is dead and in an advanced state of mouldiness, and but for the habit of examining new specimens with a low-power microscope before treating them in any other way, I should certainly have begun operations by endeavouring to clean off the 'mould'."

(e) *Resemblance to a pupa attacked but discarded as distasteful.*

The Nymphalid, *Limnitis populi* L., always pupates on the upperside side of a poplar leaf and always in the most exposed position, at the edges of woods and never in them, that is, in just those places most frequented by birds. If the sapling is not very tall, it pupates on the top, whereas if the tree is tall it often pupates well below the top but on the leaves of branches that project out the furthest and are very exposed. Before pupation the caterpillar attaches the stalk of the leaf to the twig with silk and the leaf cannot therefore fall to the ground if it later becomes detached. A silken mat is spun on the upperside of the leaf, and the edges of the leaf are bent upwards in such a way that only the dorsal surface of the pupa is visible from a lateral view. The pupa is always in the centre of the leaf with its head directed towards the tip. The large pupa is whitish yellow with

Figs. 2-3. (2) Pupa of *Spalgis epius* Westwood. (After Aitken). (3) Pupa of *Spalgis lemolea* Druce. (After Holland).

numerous black spots on its exposed parts. On the dorsal base of the abdomen there is a large gibbosity which is orange-yellow, shiny, and semi-transparent. The cuticle behind the gibbosity is mat, whereas that in front of it to the head is highly polished. According to Portschinsky (1890), the appearance of the pupa is such as to suggest that some animal, probably a bird, has broken the top of the base of the abdomen entirely destroying the upper part of the first segment so that its cuticle with the black spots is scattered about or floating on the expelled yellow liquid. Part of the contents of the pupa have oozed out to form the large and semi-transparent gibbosity, and, owing to the fact that the pupa is so orientated that its head end is inclined downwards towards the tip of the leaf, some of the liquid has flowed forwards over the fore part of the pupa, which is here highly polished and appears to be covered by a liquid film. Behind the gibbosity, however, the pupa is mat, nor would any liquid be expected to flow in this direction, which is against gravity.

Birds and other vertebrates have to learn by experience the significance of aposematic colours, so that there is nothing inherently improbable in Portschinsky's explanation: under natural conditions a small per centage of aposematically coloured insects are attacked and then discarded. This is a common enough result in experiments with domestic animals.

(f) *Resemblance to bird excrement.*

Droppings of birds, lizards, and caterpillars are such common objects in nature that it should occasion no surprise that a fairly large number of species mimic them. However, a resemblance to excrement appears to be uncommon amongst pupae, and the only instance of such a resemblance known to me is that of the European Lycaenid, *Strymonidia pruni* L. (Portschinsky, 1890).

(g) *Resemblance to an inflorescence.*

According to Jordan (1924), the pupae of the Brazilian Erycinid, *Mesosemia sylvina* Bates, are fastened by the tail in an upright position to the stem or twig of a herbaceous plant. They are so arranged in clusters of three along a stalk that the whole resembles a verticillate inflorescence with seed pods or dried up buds.

(h) *Resemblance of the pupa to its larva.*

I have recently (Hinton, 1955a) given an account of one of the most interesting instances of mimicry known to me, namely, the mimicry of the pupae of two subfamilies of the Psephenidae, the Eubrianacinae and the Psephenoidinae, to their respective larvae. Both larvae and pupae of these are aquatic, and I know of no other instance of mimicry amongst aquatic insects.

The larvae of the Psephenidae are not attached to the substrate, but their round or onsciform shape is such that the faster the current of water the more firmly they are pressed onto the substrate providing only that they do not slip. Slipping is prevented by a marginal fringe of friction setae. Whenever the larvae move out from beneath stones so that they are exposed to the current in the rapid streams in which they live, they are firmly anchored to the substrate. Fish do occasionally eat larvae. For instance, in North America it was found that the larva of *Psephenus herricki* DeKay was eaten,

but only rarely, by white suckers (*Catostomus* sp.), and West (1929, p. 15) says: "Obviously only such a mouth as that possessed by a sucker would be able to successfully pry loose such an adhesive larva, hence the danger from predaceous fish must also be slight . . . Furthermore, suckers tend to frequent muddy bottoms, while the *Psephenus* larvae are usually found on rocky bottoms . . ."

The pupae are glued very firmly to the substrate, and the selective value of their resemblance to the larvae would seem to lie in the fact that fish or other vertebrates have to learn only one form and pattern instead of two, and so fewer attempts to pry off the pupae are made. The capacity of form discrimination by fish is adequate to this explanation.

The resemblance of the pupae to the larvae is achieved by quite different means in the two subfamilies. In the Eubrianacinae, only the last three segments of the larval cuticle are shed, and the whole anterior part is attached to and remains as a covering over the pupa. The shed segments of the larval cuticle are replaced by heavily sclerotised pupal structures which, from a dorsal view, so closely resemble the missing parts of the larval cuticle that the latter appears to be complete. Thus, from a dorsal view, a fairly close examination is required to distinguish the larva from a larval cuticle containing a pupa. The tergites of the pupa, other than the last three, are thin, pale, and very slightly sclerotised. The marginal fringe of frictional setae of the larval cuticle is apparently continued without interruption on the three apical abdominal tergites of the pupa. But on the pupal tergites the marginal fringe consists entirely of sharp and deep indentations of the margin amongst which are no setae. Perhaps the most unexpected resemblance between the pupa and larva concerns the eighth abdominal spiracles. These are non-functional in the pupa, but the spiracular scars are unusually large and the cuticle peripheral to the scars is so pigmented that a very good approximation to the appearance of the functional spiracles of the larva is produced. The resemblance between abdominal segments 7-9 of the pupa and the corresponding segments of the larva is thus much enhanced.

In the Psephenoidinae the last larval cuticle is entirely shed, and the resemblance between the two stages extends to the whole dorsal surface of the pupa (compare figs. 1 and 3 of pl. 1, Hinton, 1939). The resemblance to the unusually modified eighth and ninth segments of the larva is achieved not by comparable modification of structure but only by a colour pattern.

In sharp contrast to these pupae that are found in the same places as their larvae are those of *Psephenus*. *Psephenus* quits the water to pupate, and generally does so under a stone. The larval cuticle is not shed, and the pupa itself is entirely pale, feebly sclerotised, and in no part resembles the larva. The retention of the larval cuticle can hardly serve as a defence against vertebrates but may, perhaps, be a mechanical protection against some of the other arthropods found beneath stones.

V. NON-PASSIVE PROTECTIVE DEVICES

The protective devices that necessarily involve some activity on the part of the pupa or the pharate adult, or both, are the pupal mandibles, gin-traps, stridulatory or other structures used in sound production, ant-attractant glands, and the use of spines on, or poison reservoirs in, the larval cuticle.

A. Pupal mandibles

The most primitive of recent endopterygote pupae are the decticous pupae of the Megaloptera, Neuroptera, Zeugloptera, Trichoptera, Lepidoptera-Dacnonypha, and the Mecoptera. In all these groups the adult escapes from the pupal cell or cocoon with the aid of the mandibles of the pupal cuticle, which are strongly sclerotised and articulated to the cranium. In all these the anterior part of the head is relatively strongly sclerotised and so provides a rigid framework that does not collapse under the force exerted when the mandibles are used by the pharate adult. The way in which the pupal mandibles are operated by the pharate adult has already been described (Hinton, 1946a): they are not operated by variations in turgor pressure as has been suggested by others, *e.g.* Thienemann (1905). The mandibular muscles of the pupal stage are never inserted in the mandibular apodemes of the pupa. At the time that the adult cuticle is formed, these muscles for the first time secure their attachment to the cuticle, but of course to the adult cuticle and not to the pupal. The mandibular apodemes of the adult fit closely around the mandibular apodemes of the pupa like sleeves (fig. 4), and there appears to be very little play between the two. For this reason movements of the adult mandibular apodemes brought about by the muscles of the pharate adult move the pupal mandibles much as if these muscles were inserted directly in the apodemes of the pupal mandible. It may be noted that none of the other pupal mouth-parts is articulated to the cranium.

The chief selective value of the mandibles of decticous pupae concerns their use in the escape of the adult from the pupal cell or cocoon. In some recent forms, for instance, those Trichoptera with hypertrophied and twisted mandibles, this may be their only value to the insect. But in many other species the pupal mandibles also play a part in defence, as is very evident from experiments with *Sialis* and *Raphidia*. In these and others the pharate adult is capable of biting severely with the pupal mandibles.

The pupal mandibles con only play a part in the defence of the pharate adult: they do not function in the pupal stage. The exact duration of the pupal stage does not appear to be known for any decticous pupa. It is probably very short, and it is not beyond the bounds of possibility that it may take place entirely within the larval cuticle, as it has recently been shown to do in some Tipulidae (Hinton, 1955). In *Myrmeleon europaeus*, for instance, the pupal stage begins 14 days before the larval cuticle is shed (Sundermeier, 1940), and the pupal cuticle is more or less detached from the epidermis within 24 hours after the larval cuticle has been shed. Thus, within these 24 hours the pharate adult phase is initiated.

B. Gin-traps

The organs called gin-traps are widely distributed in the Coleoptera and occur in some Lepidoptera. They are frequently very conspicuous, but their function seems to have been discovered only relatively recently (Hinton, 1946b) although their form has often been noted in the past. Riley (1882) supposed that those of the Sphingidae were sound-producing organs; and in her comparative study of lepidopterous pupae Mosher (1916) calls them spiracular furrows and says: "They are usually separated by sharply carinate ridges and are of various types, but their function is unknown.

The gin-trap is essentially a means of defence against animals much smaller than the pupae. An effective gin-trap requires so slight a modification of previously existing structures, and small insects and mites that are predaceous are so numerous, that it is perhaps surprising that gin-traps are not more widely distributed.

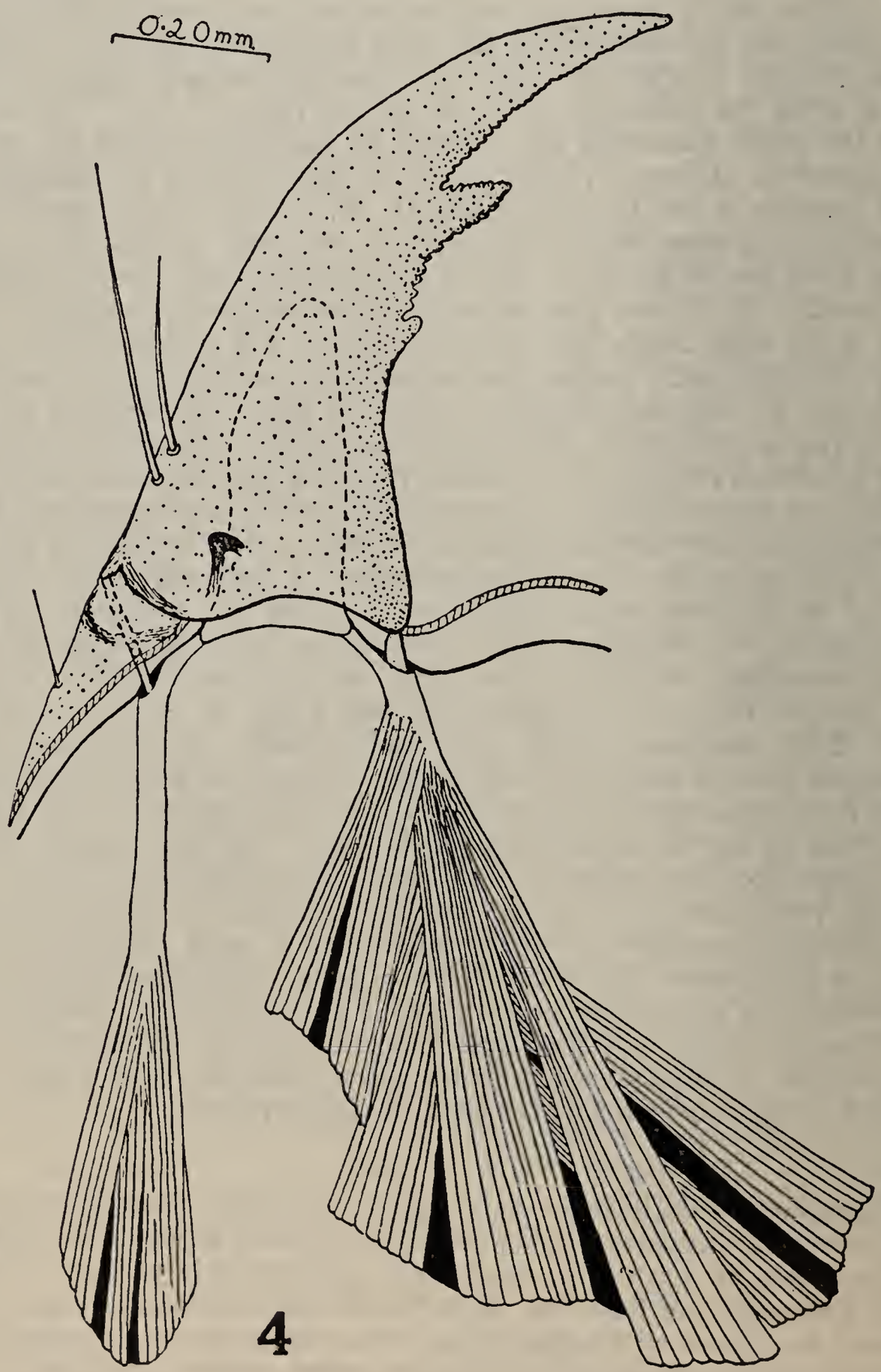


Fig. 4. Dorsal view of left mandible of *Rhyacophila dorsalis* Curtis, to show the relation of the pupal mandible to that of the pharate adult. (After Hinton).

The circumference of most abdominal segments is less where they are joined to the segment before or behind than it is at the middle (figs. 5-9). It therefore follows that the region near the posterior margin of one segment and that near the anterior margin of the segment immediately behind is always depressed. The evolution of a gin-trap involves no more alteration than a local deepening of the depression and a local hardening or sclerotization of the margins or rims of the depression. Sometimes it involves no more than the latter alteration. The chief stages in the evolution of a gin-trap are shown diagrammatically in figs. 5-9.*

The gin-traps of the pupal cuticle are always confined to the abdomen: it is only the abdominal segments that can be moved by the pupa; and, since in the pupal cuticle it is only the joints between some of the abdominal segments that are freely movable, it is only such segments of the pupal cuticle that can be moved by the pharate adult.

Different types of gin-traps have been distinguished (Hinton, 1946b), and a summary of their distribution is as follows:

I. Median or dorsal gin-traps

A. Single (fig. 10).

Coleoptera

Dermestidae: most species (Hinton. 1946b).

Ptilodactylidae: *Anchytarsus*, *Ptilodactyla* (Hinton, 1946b).

Dryopidae: *Dryops*, *Helichus* (Hinton, 1946b).

Coccinellidae: many species (Hinton, 1951).

Lepidoptera

Phalaenidae: *Labanda* sp. (Sarrothripinae) and *Carea angulata* F. (Careinae) (Hinton, 1948a).

B. Paired (fig. 11).

Coleoptera

Scarabaeidae: most Dynastinae, some Rutelinae (Hinton, 1946b).

Psephenidae: some Eubriinae (Hinton, 1946b; 1955a).

Cucujidae: *Hectarthrum* (Hinton, 1946b). Previously recorded (Graveley, 1915) as organs of unknown function.

Cerambycidae: some Prioninae (Hinton, 1946b; Duffy, 1953) and some *Phryneta* and *Phrynetopsis* in the Lamiinae (E. A. J. Duffy, personal communication).

II. Lateral gin-traps (figs. 12-13)

Coleoptera

Tenebrionidae: many species (Hinton, 1946b).

Colydiidae: *Aulonium trisulcum* Geoff.

Lepidoptera

Geometriidae: many species.

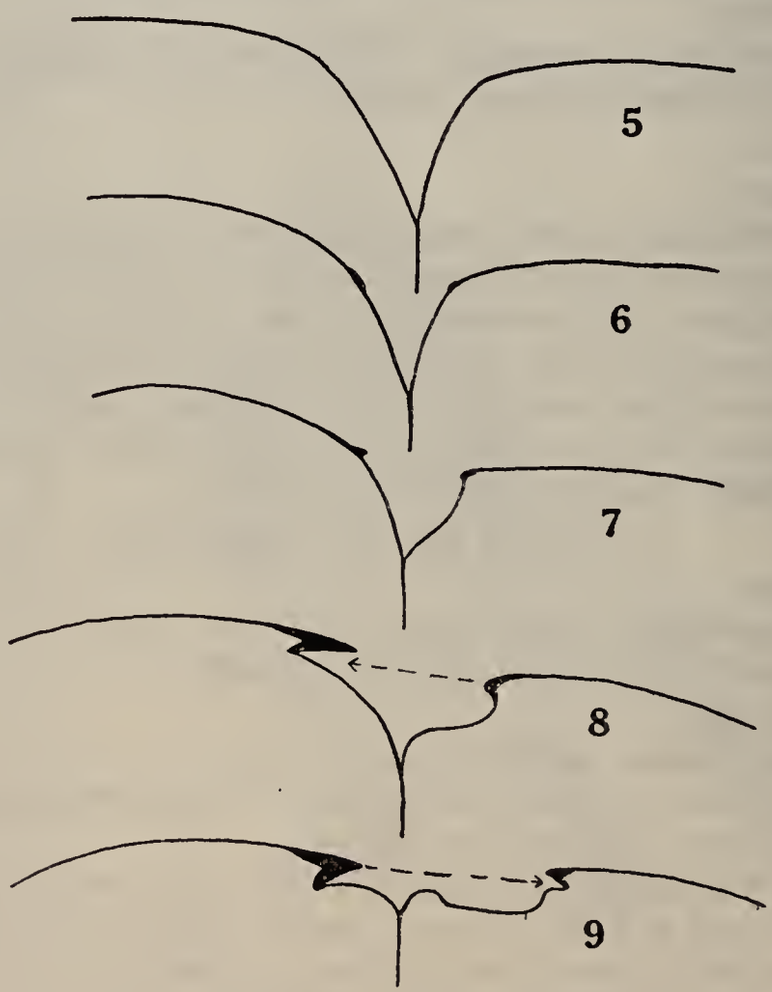
Sphingidae: species of *Sphinx*, *Platysphinx*, *Herse*, *Ceponodes* (Hinton, 1948a), and others.

The difference in position of the median and lateral gin-traps is related to a difference in the way the pupae of pharate adults move when stimulated. The resting position of pupae with dorsal or median gin-traps is normally

* Gin-traps are not confined to pupae. Abdominal gin-traps have recently been recorded (Hinton, 1955a) in the larvae of beetles of the subfamily Eubriinae (Psephenidae).

with the abdomen curved downwards so that the jaws of each gin-trap are held widely open. When the pupa is stimulated, the abdomen is bent upwards, and the segments are partly telescoped into each other so that the jaws of the gin-traps meet or overlap. In beetle pupae with lateral gin-traps the jaws of each gin-trap are borne on projecting lateral flanges of the segments, so that between each pair is a considerable drop, which serves the function of the depression between the jaws of the single and paired median gin-traps. When pupae with lateral gin-traps are stimulated, the abdomen is moved sideways and one or more gin-traps of a side are closed. Among beetles at least, the posterior jaw of each lateral gin-trap slides under the anterior. Pupae with lateral gin-traps never exhibit the more or less exclusive dorso-ventral movement so characteristic of those with median gin-traps, although when violently stimulated the end of the abdomen of some of the lepidopterous pupae with lateral gin-traps may describe an ellipse. These differences in movement are not due to the position of the gin-traps but are primary: they determine whether a gin-trap shall develop dorsally or laterally.

Experiments have shown (Hinton, 1946b) that at least in some species, *e.g. Tenebrio molitor* L., all gin-traps on a side can be closed simultaneously or any one of the five can be closed independently of all others. In experiments with *Tenebrio* with lateral gin-traps and *Dermestes* with unpaired dorsal gin-traps, it was found that when the gin-traps were snapped shut they only remained shut for a fraction of a second: and this behaviour would



Figs. 5-9. (5-7) Hypothetical evolution of a gin-trap. (8) *Dermestes maculatus* Degeer. (9) *Dryops luridus* Erichson. (After Hinton).

seem to be characteristic of most species with gin-traps. Its value probably lies in the fact that the function of a gin-trap is merely to cause the attacker to leave the pupa alone. Even such small predators as mites were not seriously damaged when caught in the relatively very large gin-traps of *Tenebrio* and *Dermestes*. It may be supposed that were the gin-trap to remain closed for any appreciable time upon the leg or other appendage of a predator, the pupa might well be damaged in the attempts of such a predator to free itself.

C. Stridulatory organs and other ways of producing sound

When we refer to sound producing organs we usually mean organs that are specialised for sound production. That is, organs which have already had a long evolutionary history and are now recognisable at a morphological level as sound producing organs. But any movement of the insect causes a disturbance in the air that results in a local increase of pressure and a displacement of contiguous molecules. These changes of pressure or displacement are called sound. It seems fairly obvious that sound produced incidentally to other activities may secondarily come to be of importance to the insect. For instance, some insects recognize each other by their wing-beat frequency; and it is taking no great risk to suppose that the wing-beat frequency is primary and that only later in the evolutionary history of the group does the insect come to behave in such a manner that the observer is certain that the particular wing-beat frequency is not only heard but is distinguished by the insect from the other sounds available in its normal environment.

Most of the sound producing organs in insects, as in other arthropods, are stridulatory organs. A stridulatory organ consists of two roughened surfaces which rub or can be made to rub against each other; and there are hardly two parts of the body which rub, or can be made to rub against each other, that are not developed to form a stridulatory organ in one group or another. It is possible to believe, and indeed it seems to me likely, that all or very nearly all stridulatory organs first developed between two parts of the body that were rubbed together in connection with some quite different activity. The secondary modification of a pupal gin-trap to form a stridulatory organ (p. 77) is a case in point.

When an insect has a sound organ that by its structure is recognizable as such, it means that the sounds produced by the organ now have, or have had in recent past,* a biological significance, that is the sounds now have,

* When the relations between an organism and its environment change so that some structure or other characteristic of the organism ceases to have a selective value, that structure or characteristic is sooner or later lost. The speed of loss will vary according to a great number of factors: whether it is biologically neutral (except for the energy involved in its production) or actively selected against, the magnitude of the alterations necessarily involved in its loss, and so on. This phenomenon is what Waddington calls "normalising selection" and others call "genetic homeostasis." These are unfortunate terms—I know no better ones—in the sense that they imply that during the loss of the characteristic in question both the species and the environment have remained static as well as the relations established between the species and its environment. In the short periods involved in laboratory experiments, this may be a near enough approximation, but it is certain to be misleading when we consider what actually occurs in nature. History does not repeat itself: the species that now loses a characteristic is not the same as that which had it.

or have had in the recent past, a selective value. But when we consider sounds produced by means other than specialised sound organs, the greatest caution must be exercised in attributing a biological significance to them even though they may appear to us to be very "deliberately" made. And here lies a field of research which has scarcely been touched: we know that ordinary walking, flying, and other movements produce sounds that are characteristic of the species or even of the sex; and it seems reasonable to suppose that many such sounds, often of frequencies or intensities outside the range of humans, will in the fullness of time be discovered to be of biological significance.

Sound is, by definition, a change of pressure or displacement in the air. But any movements made by the animal will also be transmitted through the substrate with which it is in contact; and it is far from certain that "sounds" transmitted through the substrate are not sometimes of greater biological

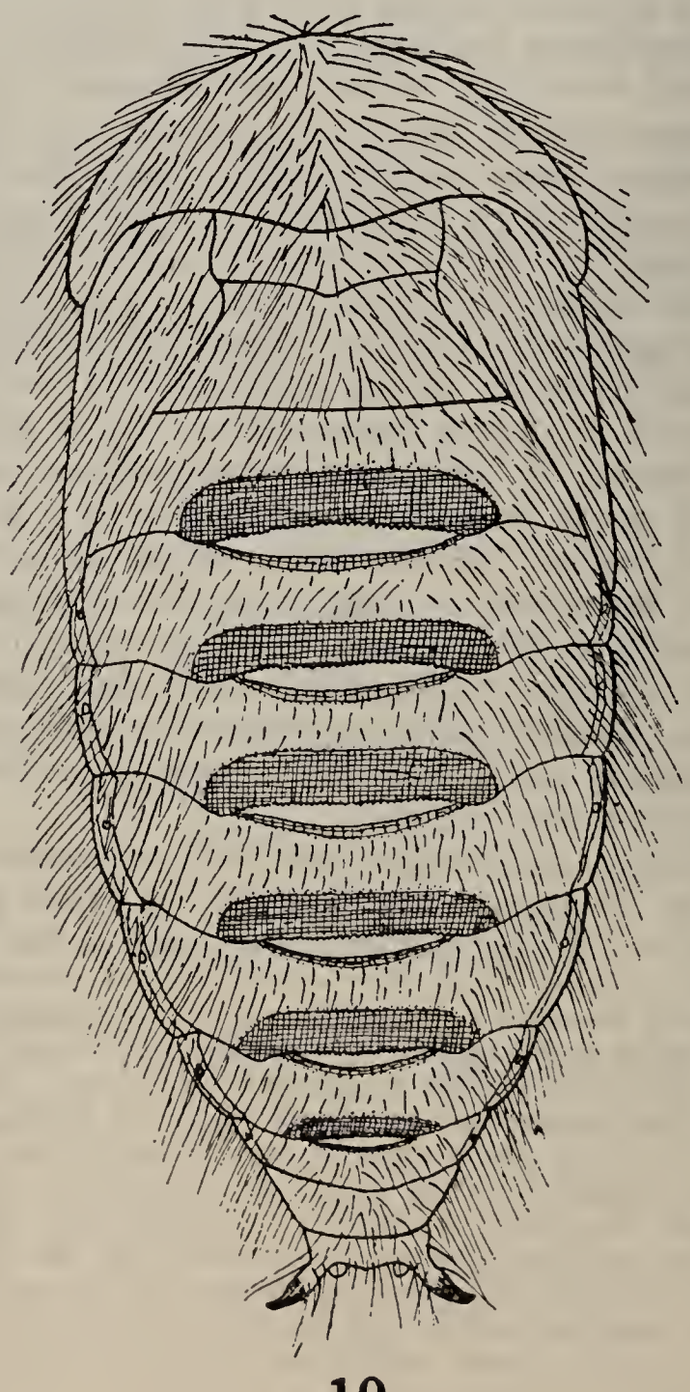


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Fig. 10. Dorsal view of pupa of *Attagenus gloriosae* F. (After Hinton).

significance than those transmitted through the air. For instance, when stridulation is not either sexual or social but only protective in significance, it is possible that changes transmitted through the substrate by the stridulating organ are of greater biological importance than those transmitted through the air. It may be that the biological effect of the stridulatory organ of a pupa is exerted chiefly through the contact rather than the distance receptors of potential enemies.

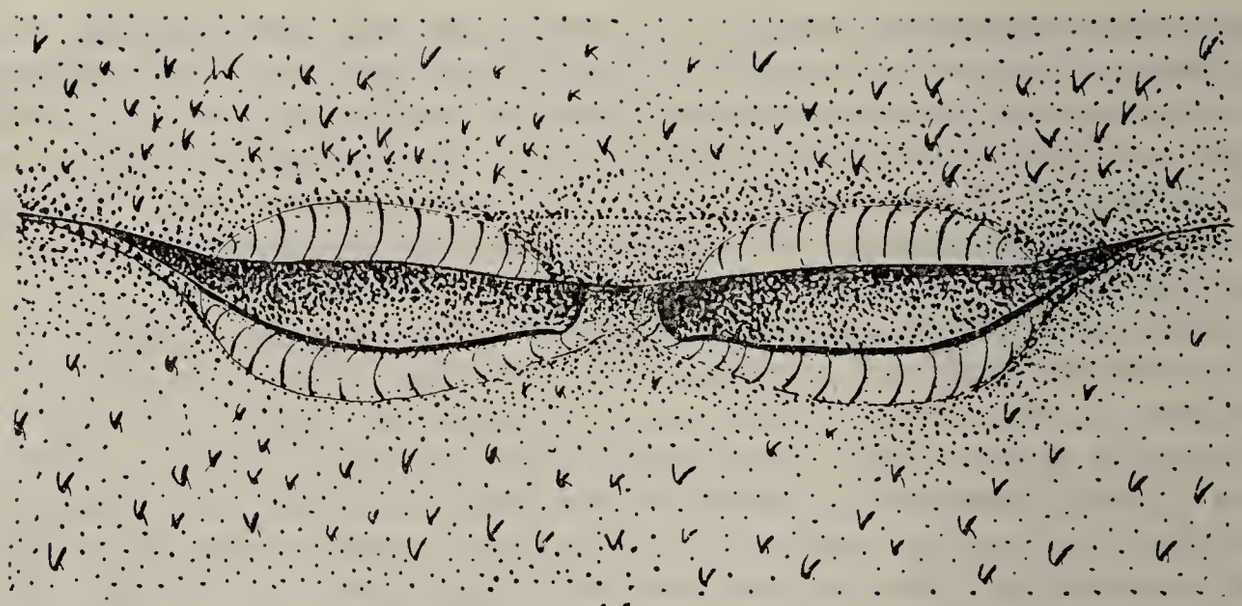
There are few records of sound production by pupae or pharate adults other than those of the Lepidoptera. Gravely (1915) heard the pupa of the Dynastid beetle, *Oryctes rhinoceros* L., stridulate; and he described as stridulatory organs those that I have called gin-traps. The fact that the jaws of the gin-traps of *Oryctes* are so sculptured that they also constitute a stridulatory organ has been confirmed by manipulation of the pupal cuticle (Hinton, 1946b). The sound is produced by friction of the lower edge of the posterior jaw on the obliquely ridged upper surface of the anterior jaw of each gin-trap. In the closely related *Dynastes* (and in other Scarabaeidae examined), the gin-traps are not modified for stridulation, from which it seems evident that the organs concerned are primarily gin-traps and only secondarily stridulatory organs.

It is possible that the late pharate adult of *Oryctes* also stridulates in another way. The adults, as is well known, stridulate by rubbing the seventh abdominal tergite, which is transversely ridged, against the tips of the elytra. In the late pharate adult phase the imaginal cuticle is fairly hard and the pupal cuticle fairly loosely attached and somewhat displaced. When the abdomen is moved by hand, the inner and heavily sclerotised ridge between the sixth and seventh abdominal tergites of the pupal cuticle is moved over the transversely ridged seventh tergite of the pharate adult, and a distinct stridulation may be heard. The pharate adult of *Dynastes gideon* L. could be made to stridulate by the same way.

An extensive account of sound production by lepidopterous pupae has recently been given (Hinton, 1948a), and it is here only necessary briefly to summarize the chief methods of sound production, of which there are a surprising number, as follows:

(1) Body knocked against the substrate or walls of pupal cell

The pupae of a number of Hesperidae and a few Lycaenidae are known to make sounds audible to humans by knocking their bodies against leaves or other objects to which they are attached or against the walls of their pupal cells. These pupae apparently have no structural modifications associated with their habit of making a knocking or rattling sound. The sounds made by pupae belonging to this category are sufficiently loud to have attracted the attention of observers, and the assumption is that the sound has a biological significance and is not merely incidental to wriggling. For instance, of the African Lycaenid, *Argiolaus silas crawshayi* Butl., Jackson (1937, p. 214) says: "When alarmed the pupa will hammer rapidly on the leaf with its head-case, making quite sufficient noise to frighten away a small predator." It must be stressed that this and other similar statements made in the literature do not constitute acceptable evidence of function. Judgement must be reserved until proof is had from rigorous experiment



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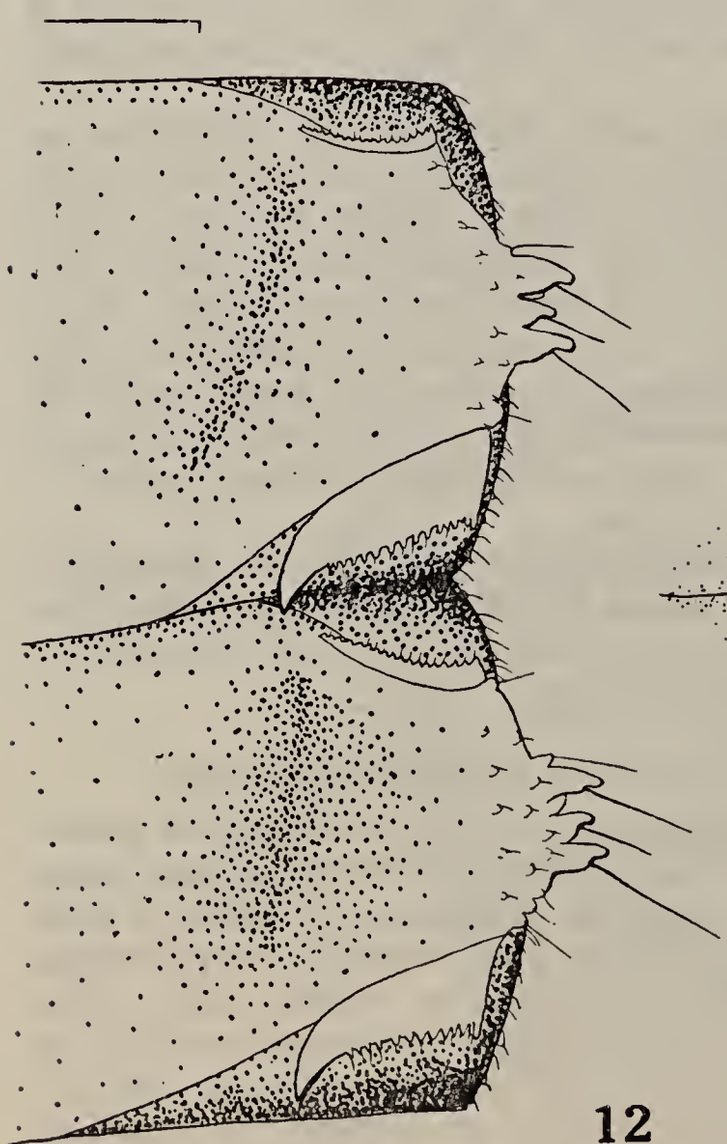

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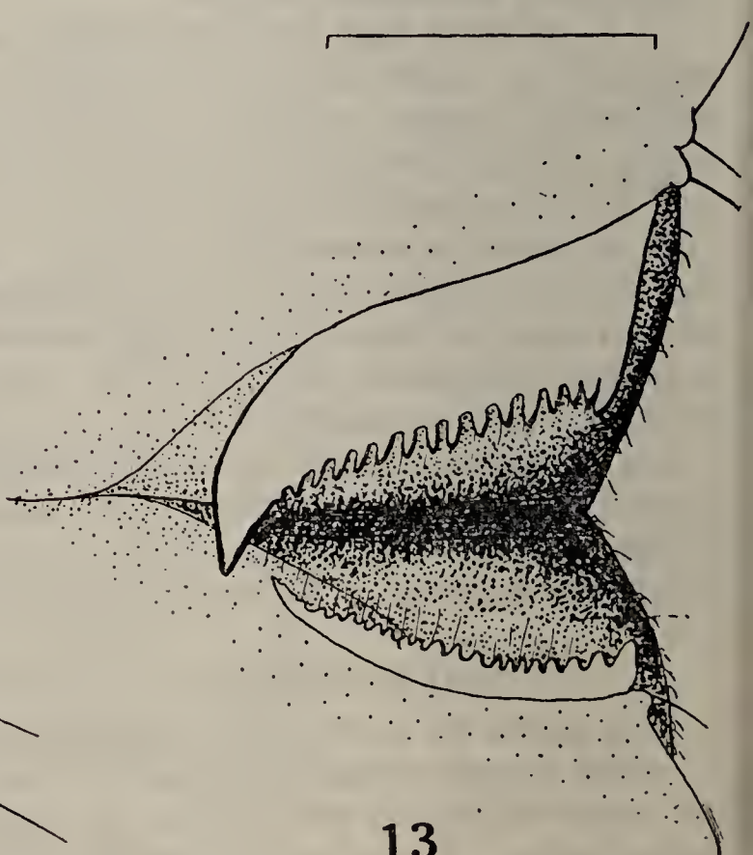

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Fig. 11. Dorsal view of fourth abdominal gin-trap of the pupa of *Ergates faber* L., Cerambycidae. (After Hinton).

Figs. 12-13. (12) Dorsal view of second abdominal gin-trap of *Alphitobius diaperinus* Panzer. Tenebrionidae. (13) Enlarged view of same. (After Hinton).

that the sounds have a biological significance and are not incidental. It is of interest to note that all the Hesperidae that belong to this section (species of *Eetion*, *Erionota*, *Matapa*, *Gangara*, and others) are Hesperiinae that pupate amongst the leaves of palm and bamboo. The two Lycaenidae are Theclinae, *Arhopala centaurus* F. and the species already mentioned.

2. Stridulatory organs on one or more pairs of abdominal segments

The most common and widely distributed method by which lepidopterous pupae produce sound is to rub one or more pairs of abdominal segments together. The stridulatory or sound producing organs consist typically of coarse transverse ridges on the anterior margin of one segment and fine tubercles on the posterior margin of the segment immediately in front. In the Lycaenidae both parts of the organ, which is between segments five and six, consist of rows of tubercles. In some Sphingidae, *Macroglossum* spp. (figs. 14-15) and *Theretra latreillei lucasi* Walk., the stridulatory surfaces also consist of tubercles. In these genera it is the anterior margin of the fifth abdominal segment which is coarsely tuberculate, and the posterior margin of the fourth which is very finely tuberculate. In other Sphingidae and in all other lepidopterous pupae known to me* the stridulatory apparatus is on segments 4-5, 5-6, and 6-7; and the posterior surface is in each transversely ridged. The stridulatory ridges may be confined to the dorsal part of the segments (*e.g. Margaronia laticostalis* Guen.) dorsum and sides (*e.g. Lymantria ampla* Walk.), sides only (*e.g.* most Sphingidae) or sides and sternum (*e.g. Gargetta viridigrisea* Dudgeon).

It has been previously noted (Hinton, 1948a) that in some Sphingidae, *e.g. Cizara sculpta* Feld., which has been heard to stridulate, the ridges of the stridulatory organ are almost as far apart as in species which definitely do not stridulate and in which the ridges constitute the posterior part of a gin-trap. It seems very likely that the transverse ridges of the stridulatory organs of some species may also function as gin-traps, but as yet there is no experimental evidence either for or against this view. In this connection it may be noted that the gin-traps of the pupae of some Dynastid beetles are secondarily modified to form stridulatory organs (see p. 77).

Some writers claim to have heard the pupa of *Acherontia atropos* L. stridulate: it has well developed transverse ridges in front of the spiracles of segments 5-7 (fig. 16). These closely resemble the stridulatory files of lepidopterous pupae known to be capable of stridulating. Nevertheless, some writers claim that it does not stridulate: the controversy is summarised by Tutt (1904, p. 432), who comes to the conclusion that the sound is made entirely by the pharate adult and the pupal cuticle is not concerned. I have not had a living pupa of this species, but I think it probable that it is capable of stridulating. If so, we may expect the pharate adult to produce sound in two different ways: by using the stridulatory organs on the effete pupal cuticle, and by vibrating the flap in its pre-oral cavity. Prell (1920) has given a good account of the "reed organ" of the adult.

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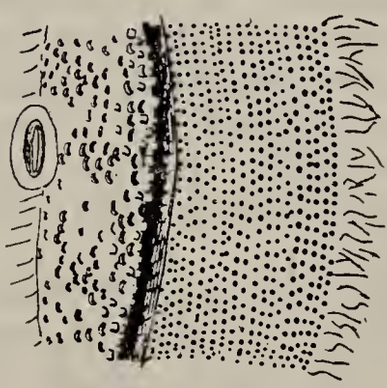
* Pyralidae, *Margaronia laticostalis* Guen., Hesperidae, *Celaenorrhinus* spp.; Paplionidae, *Papilio polytes* L. and *Troides* spp.; Phalaenidae, some species of *Plusia* and *Prodenia*; Lymantriidae, some *Lymantria* and *Dasychira*; Callidulidae, *Tetragonus catamitus* Geyer; Notodontidae, *Gargetta viridigrisea* Dudgeon; and Saturniidae, some species of *Actias*, *Holocera*, *Hylesia*, *Nudaurelia*, *Polythysania* and *Urota*.

3. Stridulatory organ on abdomen and proboscis

The only pupa known to have a stridulatory organ on the abdomen and proboscis is that of the Hesperid, *Gangara thyrsis* F. On either side of the middle of the fifth abdominal segment is a very sharp transverse ridge which is high and normal to the surface. Each ridge is curved so that its middle part is highest. The proboscis is exceptionally long and extends far beyond the end of the abdomen. It lies between, and partly resting on, the mesal part of the two ridges. When the abdomen is moved, these abdominal ridges scrape across the transverse ridges on the underside of the proboscis and produce a "hissing" sound. This species pupates in a spirally coiled cylinder made of palm leaf, and when suitably stimulated also makes a loud rattling sound by knocking itself against the walls of its pupal cell.



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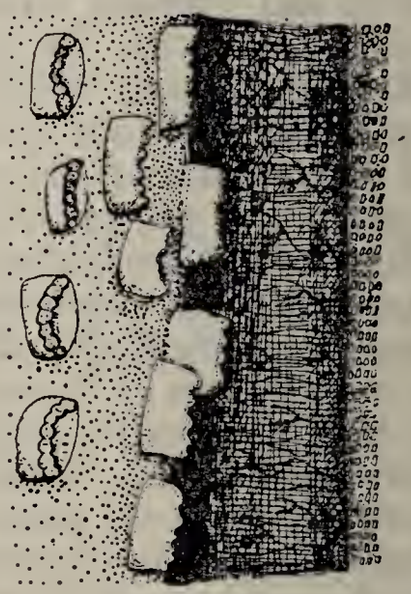

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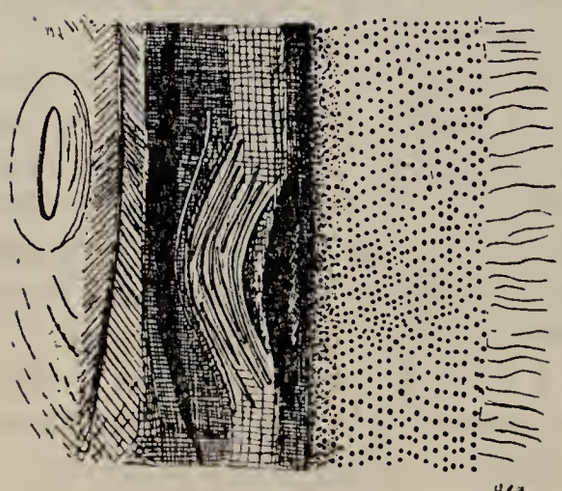

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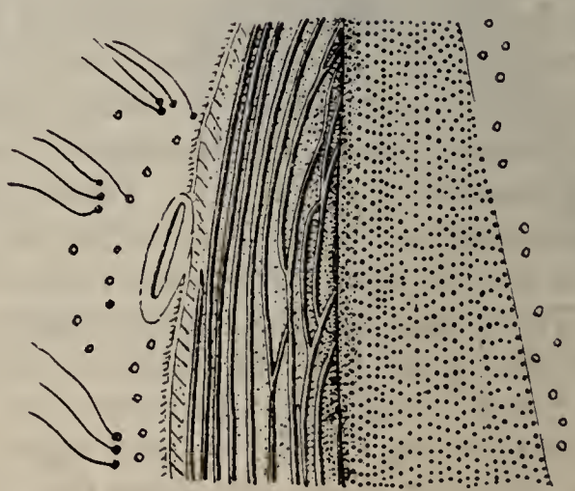

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Figs. 14-17. (14) Stridulatory surfaces of the fourth and fifth abdominal segments of the pupa of *Macroglossum corythus* Walker. (15) Greatly enlarged view of same. (16) Stridulatory surfaces of fourth and fifth abdominal segments of the pupa of *Acherontia atropos* L. (17) Same of *Lymantria viola* Swinhoe. (After Hinton).

4. Stridulatory organs on pupa and walls of cocoon

Movements of pupae that are enclosed in cocoons of stiff parchment-like silk are generally audible to humans. For instance, many Zygaenidae produce quite loud scraping noises by rubbing their backwardly directed spines against the inner surface of their cocoons. These spines are used during the emergence of the adult. They are a primitive feature of obtect lepidopterous pupae (Hinton, 1946a). The parchment-like type of cocoon is phylogenetically much more recent than the backwardly directed spines, and for this reason it cannot be said, in the absence of experimental evidence, that the sounds produced by rubbing the spines against the cocoon when the pupa is caused to wriggle have some biological significance. In the Phalaenid subfamilies Sarrothripinae and Careinae, however, the pupal cuticle is not protruded on the emergence of the adult, and the surface of the cuticle has ridges or tubercles not found in the Phalaenidae that have the normal type of cocoon. In no Phalaenidae known to me is the pupal cuticle protruded on emergence. According to the nature of the stridulatory organs, the 26 species examined by me may be grouped as follows: (a) cocoons without ridges on the inside wall, as in most Sarrothripinae and Careinae; and (b) cocoons with ridges on one or both ends of inside wall, as in some Sarrothripinae.

(a) *Cocoons without ridges on inside wall.*

The cocoons which belong to this group all have a definite vertical, anterior escape valve. The pupae of all species have the dorsal areas of the head, thorax, and part of all of the abdomen more or less densely set with small to moderately large, erect tubercles, which are distinctly flat-topped in some species. The ventral and ventro-lateral areas are smooth except for the fifth abdominal sternum which, except in *Risoba basalis* Moore, has tubercles as large as those of the fifth tergum but sparser. The dorsal tuberculate areas are often narrow, but whether wide or narrow contrast sharply with the smooth lateral and ventral areas, as there is no obvious zone of transition between the two. Species of *Labanda*, *Blenina*, *Symintha*, *Gariga*, *Paracrama*, and *Pseudoips* have a scraper on the tenth abdominal segment. This consists of longitudinal ridges. Some species have as many as 80 such ridges and others as few as seven. The ridges of the scraper may extend most of the way around the segment or may be confined to the dorsal or lateral parts, or both. They may be well developed or low and irregular, as in *Pseudoips bicolorana* Fuessly. *Risoba basalis* Moore, which has no longitudinal ridges on the tenth abdominal segment, is unusual in having the dorsal posterior margin of the seventh abdominal segment distinctly elevated and armed with especially long tubercles normal to the surface. In *Paracrama dulcissima* Walk., which has a scraper of 26 ridges, the sculpture of the dorsal surface elsewhere consists of prominent wrinkles rather than tubercles.

The sulphur-yellow cocoon of *Labanda fasciata* Walk. (fig. 18) is most unusual in that it is constructed with a large oval opening in its dorsal side so that the dorsal parts of the first six abdominal segments of the pupa are exposed. The vertical tubercles on the exposed parts of these segments are longer and stouter than those elsewhere. The moth does not escape through

this opening but through the anterior escape valve, which, as usual has its long axis vertical.

(b) *Cocoons with ridges on inside wall.*

Some Sarrothripinae construct longitudinal ridges of silk on the dorsal inside wall of the cocoon near its posterior end (figs. 19-20). These ridges, which are very hard, are so placed that they lie above the tenth abdominal

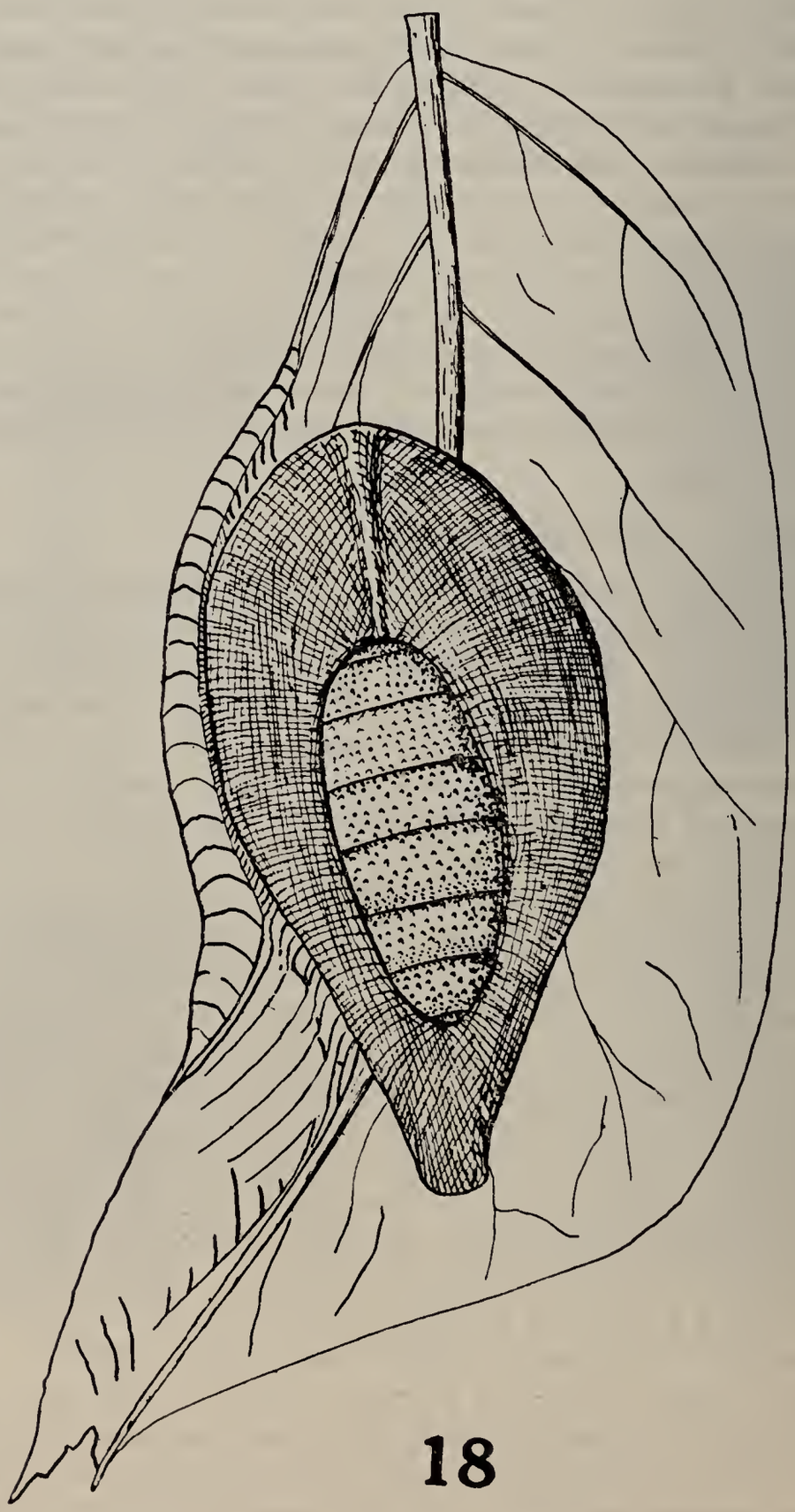

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Fig. 18. Cocoon of *Labanda fasciata* Walker. (After Hinton).

segment of the pupa, the dorsal surface of which has a transverse row of relatively short longitudinal ridges (fig. 21). Both the pupa and pharate adult are able to wriggle in such a manner that a loud sound is produced when the scraper on the tenth segment of the pupal abdomen is rubbed across the longitudinal silken ridges previously constructed by the larva on the inside of the cocoon. Fletcher (1919) appears to have been the first to describe this type of stridulatory organ. The sound produced by the pupa or pharate adult of *Eligma narcissus* Cr. is described by Hemmingsen (1946) as, "a stridulating sound produced at a somewhat slower rate than the grasshopper calls usually heard there [North China]. Also the tone was more hissing."

The Sarrothripinae known to construct silken ridges on the inside of the cocoon are species of *Eligma*, *Selepa*, *Plotheia*, *Iscardia*, and *Gadirtha*. The pupae of these species may have ridges on other segments beside the tenth abdominal, but they never have the erect tubercles of the Sarrothripinae and Careinae that do not build ridges on their cocoons. The sides of the segments on which the accessory ridges occur sometimes project outwards beyond the general level of the body, and such ridges may function as scrapers but do not of course come into contact with the ridges spun on the inner wall of the cocoon. The Sarrothripinae that have ridges on the cocoon also have the three posterior segments of the abdomen narrower in relation to the anterior segments than those species that do not have ridges on the cocoon (fig. 21). Owing to this constriction, the arc through which the tip of the abdomen may travel when the pupa wriggles is greater.

The Indo-Australian species, *Gadirtha pulchra* Butl., is exceptional in that the caterpillar constructs a series of longitudinal ridges at both ends of the cocoon. To understand the significance of this, it is necessary to consider for a moment the escape apparatus.

In the Sarrothripinae that do not build ridges on the inner wall of the cocoon, the escape apparatus is a definite and obvious structure at the anterior end of the cocoon. In the Sarrothripinae that build ridges on the inner wall of the cocoon, the escape apparatus is merely a flimsy area at the anterior end through which the moth bursts on emergence. There is a greater or lesser period, according to the species, after the cocoon is completed before the caterpillar pupates. During this period it is possible for the caterpillar to turn around, so that when it finally pupates the head of the pupa is at the posterior end of the cocoon instead of at the anterior. When the successful emergence of the moth depends on an escape apparatus constructed by the caterpillar, the moth fails to emerge and dies in the cocoon if the caterpillar has turned around the wrong way before pupating. Under natural conditions moths sometimes die for this reason, as most naturalists will know and as was first noted by Réaumur in 1734.

The significance of having both an escape apparatus and longitudinal ridges at both ends of the cocoon would seem to be that if for some reason or another the caterpillar comes to lie with its head at the posterior end of the cocoon and pupates in this position, no harm results: its pupa and pharate adult are able to stridulate and the moth is able to emerge regardless of whether the head is in the anterior or the posterior end of the cocoon.

D. Ant-attractant glands

Social insects protect their nests and to some extent the trophoporic fields surrounding them from the attacks of other animals; and this protection is one of the obvious advantages automatically gained by any arthropod that can exist in one way or another in the nest or in the trophoporic field surrounding the nest. Some species that normally exist with ants are provided with glands that secrete a substance attractive to ants. It therefore seems

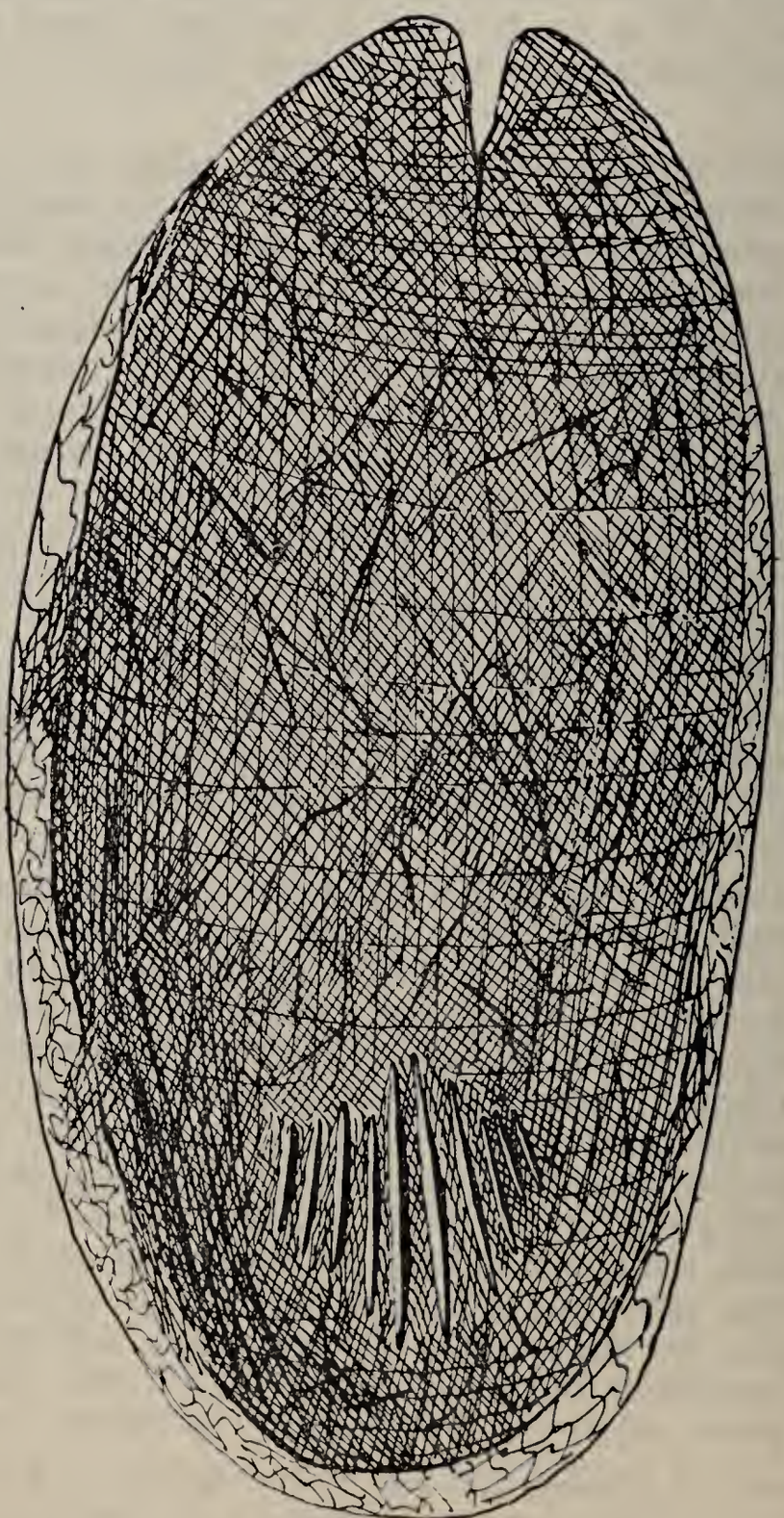

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Fig. 19. Inner dorsal side of cocoon of *Selepa celtis* Moore. (After Hinton).

reasonable to suppose that the function of the glands is to secrete such a substance, and that the selective value of the glands lies in the fact that in providing ants with a secretion they confer upon the insect a certain immunity from attack not only by the ants but also from many other potential enemies owing to the presence of the ants.

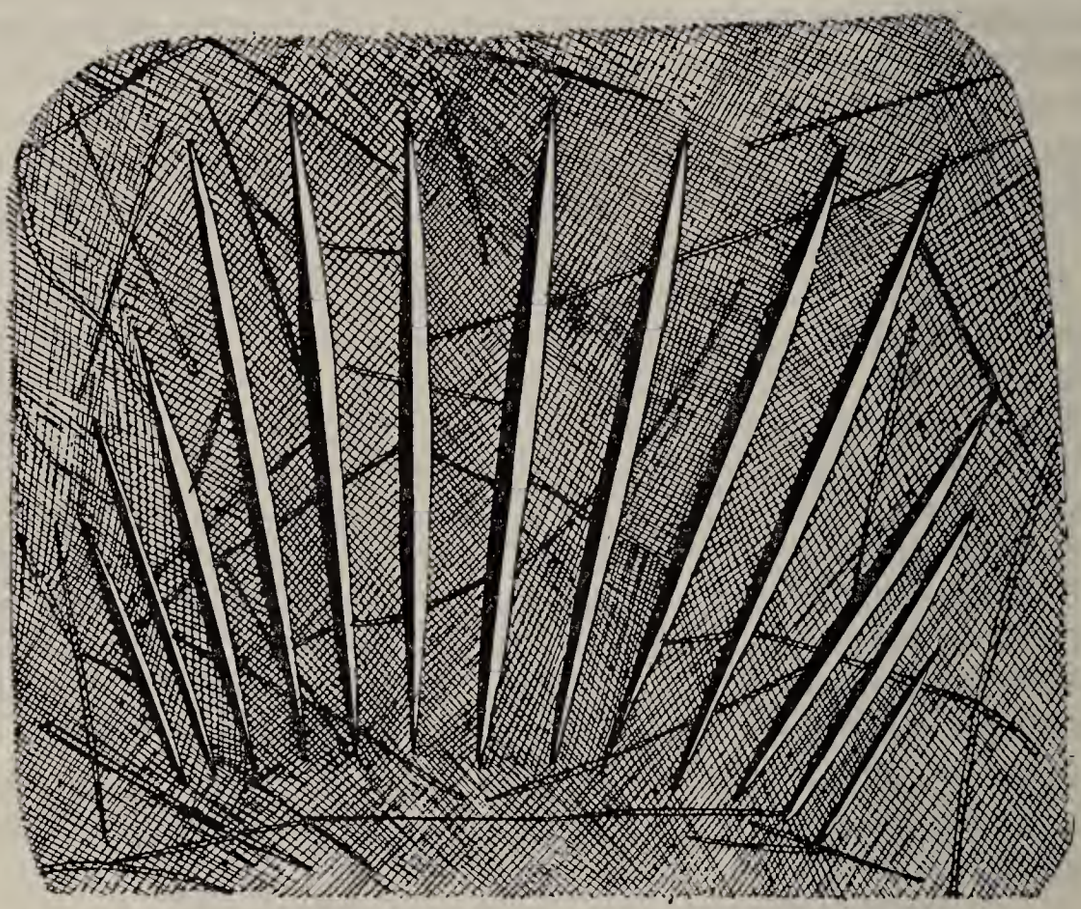
The pupae of many Lycaenidae that have myrmecophilous larvae are attended by ants, *e.g.* species of *Aslauga* Kirby, *Lachnocnema* Trim., *Miletus* Hübn,. *Arhopala* Boisd., *Chilaria* Moore, *Hypolycaena* Feld., *Thaduka* Moore, *Zesius* Hübn., *Castalius* Hübn., *Euchrysops* Butl., and *Jamides* Hübn. The pupae of all these species are said to have glands that secrete an ant-attractant substance, but in no single instance has more than the presumed orifice of the secreting organ been described. In nearly all of them there is what appears to be the orifice of a gland on the dorsum of the seventh abdominal segment. The balance of evidence suggests that, at least in some pupae, an ant-attractant substance is secreted through this orifice. In *Miletus boisduvali* Moore there is said to be an ant-attractant organ opening on either side of the seventh abdominal segment as well as one on each side of the prothorax (Roepke, 1918). For an extensive summary of the literature on Myrmecophilous Lycaenid pupae the reader is referred to Hinton (1951a).

The pupae of some Riodinidae are also attended by ants, and, according to Bruch (1926), the pupa of *Hamearis epulus signatus* Stich. of Argentina has ant-attractant glands.

E. Poison reservoirs in attached larval cuticle

A few flies and many Lepidoptera and beetles pupate on leaves and other exposed surfaces and have no cocoons. These often retain the cuticle of the final instar larva attached to their posterior abdominal segments. Little is known of the significance of this habit. I have been unable to discover the biological significance of the habit in some species, but in others it is a method of attaching the pupa to the surface, or a protective device against predators, or both. Sometimes the final larval instar cements its posterior segments to the surface. The pupa subsequently formed frees itself of the anterior part of the larval cuticle and is held to the leaf or other surface in this way. The origin of the cement is not known. It may sometimes be the secretion of the labial glands, as is, for instance, the cement used by *Drosophila* to fix its puparium to the substrate (Fraenkel and Brookes, 1953). It is probable, however, that it is sometimes a product of the alimentary canal or the Malpighian tubes, especially amongst beetles, all of which lack labial glands in the larval stage. For instance, some Chrysomelidae cement their earthen pupal cells with a product of the anterior part of the gut, *e.g. Lema melanopa* L. (Venturi, 1949).

The mature larvae of some Chrysomelid beetles of the subfamily Chrysomelinae have large paired cuticular reservoirs on the last two thoracic and first seven abdominal segments. The external opening of each reservoir is on the apex of a large lateral tubercle. Each reservoir receives the secretion of numerous pyriform glands (fig. 22). The secretion of the glands is probably salicylaldehyde, which is known to be secreted by the homologous glands of other Chrysomelinae that feed on willow and sallow, *e.g. Chrysomela*



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Figs. 20-21. (20) Silken cocoon file of *Eligma hypsoides* Walker. (21) End of abdomen of the pupa of the same species drawn to the same scale. (After Hinton).

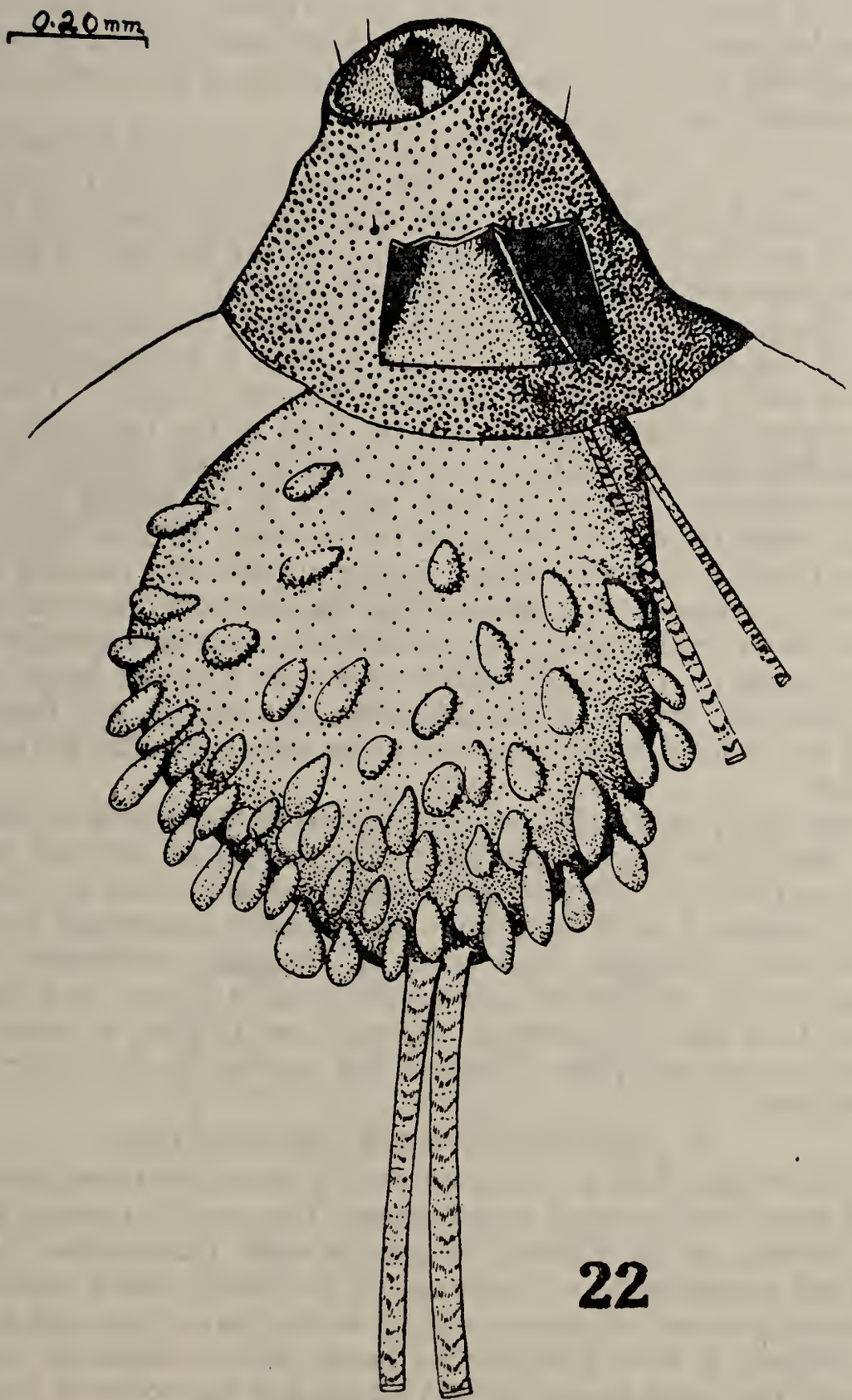

Fig. 22. *Chrysomela tremula* F. Mesothoracic glands of third instar larva. Some of the pyriform glands have been detached. (After Hinton).

populi L. (Claus, 1861), *C. lapponica* L. (Garb, 1915), and *Phyllodecta vitellinae* L. (Wain, 1943).

At the larva-pupa moult the cuticular linings of the reservoirs retain their contents. The pupae and pharate adults of *Chrysomela cuprea* F. (Portschinsky, 1890) *C. tremula* F. (Portschinsky, 1890; Hinton, 1951), and *Plagiodera versicolora* Laichart (Hinton, 1951), and perhaps many other Chrysomelinae, make use of the poison contained in the reservoirs of the larval cuticle in a manner unknown in other insects.

Before pupation the larvae of *Chrysomela tremula* attach themselves head downwards on a leaf or stem and thus when they pupate the pupa must also hang head downwards. The pupa splits the larval cuticle as far as the metathorax and then pushes it posteriorly until the first five or six, usually six, dorsal abdominal segments, are exposed (fig. 23).

When the pupa or pharate adult is stimulated, the dorsal longitudinal muscles of the abdomen are contracted so that it jerks upright until its long axis is nearly normal to the surface of the leaf or stem. At this time it presses against the larval cuticle, and the fluid in the reservoirs is forced out. This fluid does not spill over but collects in a large drop on the end of the larval tubercles. When the pupa returns to its resting position, the reservoirs regain their shape owing to the elasticity of their cuticle and so the drop of fluid is sucked in again. It thus appears that the only fluid lost is that lost by evaporation, perhaps chiefly in the short time that the drops are present at the end of the tubercles, unless, of course, some of it is wiped off by an attacker. The adult emerges 5-7 days after the larval cuticle is shed. During this time the shed cuticle remains flexible, and fluid may be squeezed out by hand from the reservoirs for some time after the emergence of the adult.

The pupa and pharate adult usually respond to stimulation in such a way that the fluid from the thoracic reservoirs is squeezed out and not infrequently also that from the first abdominal segment. When the response is unusually violent, a little fluid from the posterior abdominal segments is sometimes also extruded. The pupa of *Plagiodera versicolora* is much smaller than that of *Chrysomela tremula*, being 3-4 mm. long instead of 8-10 mm. It is not aposematically coloured but is black or nearly so. It does not leave its host plant to pupate but pupates on the upper surfaces of willow leaves.

F. Spines on attached larval cuticle

Some insects that have a spinose or densely setose last larval instar do not shed the larval cuticle when they pupate. This cuticle remains as a protective covering, as for instance, it does in some Dermestidae (*Anthrenus* spp.). Such protection as the retention of the larval cuticle cuticle affords these insects does not involve any activity on the part of the pupa or pharate adult. However in some Chrysomelid beetles of the subfamily Cassidinae, *e.g. Cassida*, the larval cuticle remains attached to the posterior segments of the pupa, and by movements of the abdomen the pupa or pharate adult can thrust the spines of the attached cuticle into an attacker. Whether or not under natural conditions these insects are in this way afforded some protection against the casual predators they normally encounter remains to be demonstrated by experiment.

VI. REPAIR OF WOUNDS BY TISSUE SHED AT PUPA-ADULT MOULT

At the pupa-adult moult of *Lipsothri remotax* Walk. and L. *nervosa* Edwards (Tipulidae, Eriopterini) the epithelium that secreted the cuticle of the pupal spiracular gill is cut off from the living insect by a basal membrane secreted across the orifice that effected the continuity of the haemocoele and the lumen of the spiracular gill. In *L. remota* the epithelium thus cut off in each gill includes about 1,100 epidermal cells and a quantity of cell-free blood. A detailed account of the structure of the gill has recently been given (Hinton, 1955) and will not be repeated here. The pupal spiracular gill functions as a gill throughout the pharate adult phase, although at this time it is only mechanically connected to the living insect. The duration of the pharate adult phase at 20°C. and 100 per cent. relative humidity is 9 days. I have found that during the whole of this time any small wounds made in the cuticle of the spiracular gill are repaired by the tissue isolated in it.

When the material used to repair wounds in the spiracular gill is hardened, it can be completely dispersed in a saturated solution of KOH held at 180°C. for half an hour. This would indicate that if it contains chitin, the

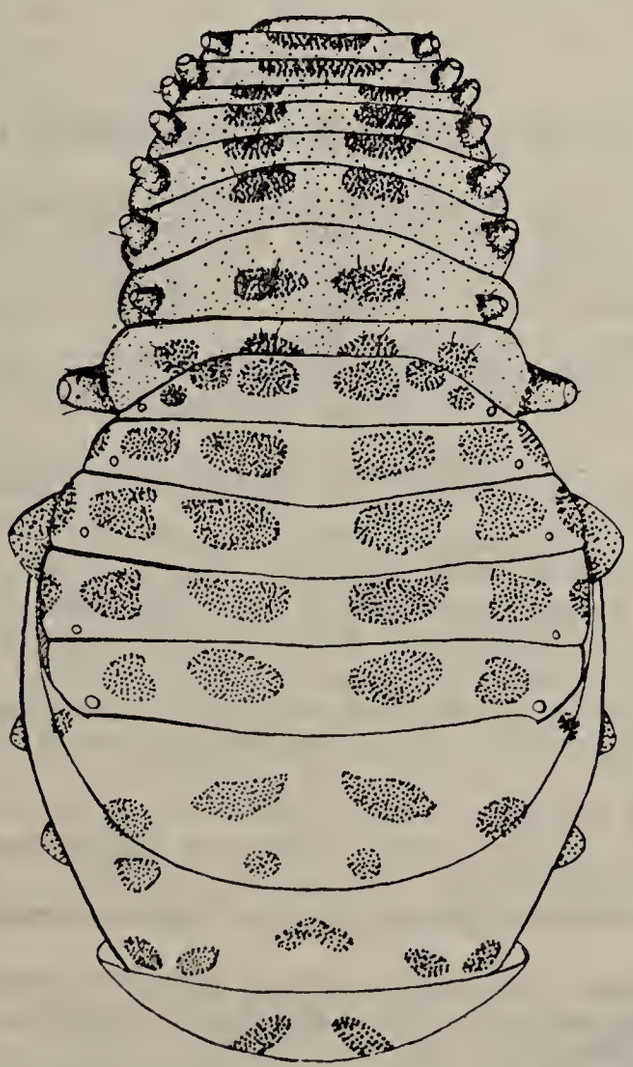

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Fig. 23. Dorsal view of pupa of *Chrysomela tremula* F. with attached cuticle of last larval instar. (After Hinton).

chitin does not form a discrete framework. The wound plug will not disperse in cold concentrated nitric or hydrochloric acid even in 24 hours. It withstands hot concentrated nitric for more than 10 minutes, but it is rapidly dispersed in nitric acid and potassium chlorate. From these results, it is reasonable to suppose that the wound plug consists chiefly of a highly tanned protein.

Not only does the isolated tissue repair wounds throughout the life of the pharate adult, but, even more remarkable, it continues to repair wounds made after the adult insect has flown away. Pupal cuticles discarded by the emerged adults were kept at 20°C. and 100 per cent. R.H. and wounded at ever increasing intervals. It was found as a result of these experiments that wounds would occasionally be repaired that were made as long as five days after the emergence of the adult.

I have recently found that the spiracular gill of *Geranomyia unicolor* Haliday, an intertidal Limoniini, is somewhat similar in structure to that of *Lipsothrix*. The epithelium or blood isolated in the spiracular gill will also repair wounds. *Geranomyia* belongs to a different group of the Tipulidae, and it is therefore evident that this method of protecting the spiracular gill has been independently evolved on at least two occasions.

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